THE OCEAN SUNFISHES (FAMILY MOLIDAE)

By A. FRASER-BRUNNER

SYNOPSIS

The relationships of the Molidae with other Plectognathi are briefly discussed. The movable lobe at the hind margin of the body, supported usually by migrant dorsal and anal rays but sometimes also by caudal rays centrally, is designated the 'clavus'. Three genera are recognized, assigned to two subfamilies. *Masturus* is shown to include two forms (treated as species but possibly the sexes of one). Evidence is presented to show that in this genus alone of the family some caudal rays are developed. *Mola* is shown to include two species, which are diagnosed and figured. Sexual dimorphism in *Mola mola* is described. Full synonymies are included.

ON account of their curious form and the great size which they often attain, the fishes of the family Molidae, usually called Ocean Sunfishes, have attracted considerable attention from early times. A large and scattered literature exists concerning them, but although comparative studies have been made from time to time and their anatomy has received attention quite frequently, we are still far from a complete understanding of their relationships. This is mainly because all the species are rather rare, and their occurrence unpredictable, so that it is not possible to make an excursion for the express purpose of collecting specimens, as could be done with many other fishes, while the great size of most examples makes transportation and preservation a difficult problem. Consequently good comparative material is not easily available for study, and much reliance has to be placed upon published descriptions and figures.

It is the purpose of the present work to draw attention to certain facts which have become apparent from a study of the literature, aided by the material in the national collection.

My thanks are due to Mr. G. Palmer for his assistance in seeking out some of the references and checking a number of points in them.

I am concerned here only with taxonomy within the family, since a full consideration of their relationship to other Plectognathous fishes will be included in a larger work upon the anatomy and phylogeny of the whole Order now in preparation. It can be pointed out here, however, that I have already indicated in an earlier paper (Fraser-Brunner, 1943), that the Molidae are not really as highly specialized as previously supposed. Their main peculiarity lies in the atrophy of the rear end of the vertebral column, resulting in a mechanical rearrangement of the median fin-structures closely resembling that seen in other fishes when the tail is amputated at an early age; some interesting examples of this among Flatfishes have been given by Chabanaud (1935). The resemblance is not quite perfect, since with amputation the supporting bones of dorsal and anal fins are lost with the tail, whereas in the Molidae only the vertebral structures are lost.

The *lateralis* muscles of the trunk, deprived of their normal attachment, become inserted upon the deep muscles of the dorsal and anal fins, and progressively lose their identity in the genera *Ranzania, Masturus, Mola*. The result of this is that body-flexion is lost but the dorsal and anal fins gain in power, and the latter are therefore

the principal means of locomotion. The posterior parts of these two fins extend round the rear end of the truncated body to support a broad, stiff lobe which acts as a rudder. This has been called the 'pseudo-caudal' by Raven (1939 a), but this is not a very suitable term in my opinion; any structure in this part of the body may be described as 'caudal', and even if 'pseudo-caudal fin' is used, this is not true for all the species, for I hope to demonstrate on a later page that remains of the true caudal fin are included in the structure in *Masturus*.

For this rudder-like lobe at the end of the body in the Molidae I therefore propose using a new term, and throughout this paper it will be called 'the clavus' (Lat. *clavus*, a rudder).

Apart from these changes of form, all of which are demanded as mechanical consequences of the phyletic atrophy of the posterior part of the vertebral column, the Sunfishes resemble in their anatomy the more primitive of the Tetraodont fishes, and in one feature at least, the retention of the fourth gill, they are less modified even than those. They stand, therefore, near the main stem of the Tetraodonts, and attempts to derive them from the highly modified Diodontidae seem to me to be very far-fetched; whatever resemblances the latter may show are more plausibly explained by the assumption that they are evolved from a *Mola*-like type (before caudal atrophy) rather than the reverse. The Molidae show also some features in common with the Ostraciontoidea alone among Plectognathi, and indicate therefore the divergence of the Trunkfishes and Puffer-fishes from a common stock during their evolution.

In my classification of the Tetraodontoidea I expressed the view that only two genera of Molidae should be recognized. This was based on the belief, current at that time, that *Ranzania*, *Masturus*, and *Mola* were each represented by a single species, and since the latter two forms seemed to be more closely related to each other than to *Ranzania*, it appeared that this relationship would be better expressed by placing them together in the genus *Mola*. A more detailed examination of these fishes, however, has caused me to modify these views.

Firstly, I find that there are two species of *Mola* in the limited sense—one of worldwide distribution and the other apparently restricted to the Australasian region. Whitley (1931) recently revived the name *Mola ramsayi* Giglioli 1883 for the latter, but was apparently unaware of its distinguishing characters and assumed that all specimens from that region should be so named, whereas his main description appears to be of *M. mola* and the records show that both *M. mola* and *M. ramsayi* are to be found around Australasia. The type of *M. ramsayi*, a huge stuffed specimen, is in the British Museum (Natural History), and by a piece of good fortune one of our spirit-specimens belongs to that species, so that I have been able to make direct comparison with examples of *M. mola* of similar size.

Secondly, a close study of the literature concerning *Masturus lanceolatus*, aided considerably by the excellent work of Gudger on this subject, reveals that two forms are included here also, though it is not certain that they are different species. More interesting is the apparent fact that in *Masturus* alone of the family a remnant of the caudal fin is included in the support of the clavus. In this and in its musculature it is a little less specialized than *Mola*, and it therefore now seems desirable to recognize

it as a distinct genus in order to express its relationship to the other genera more clearly.

There has been much speculation in the past as to whether the rays supporting the clavus belong to the caudal fin or to the dorsal and anal, and even Gregory & Raven (1934), when describing the anatomy of *M. mola*, thought them to be caudal although their description and figure indicate that they are not (an error corrected by Raven in 1939). Apart from internal anatomy, the number of these rays is in most cases against the likelihood that they all belong to the caudal fin; in most Plectognathi
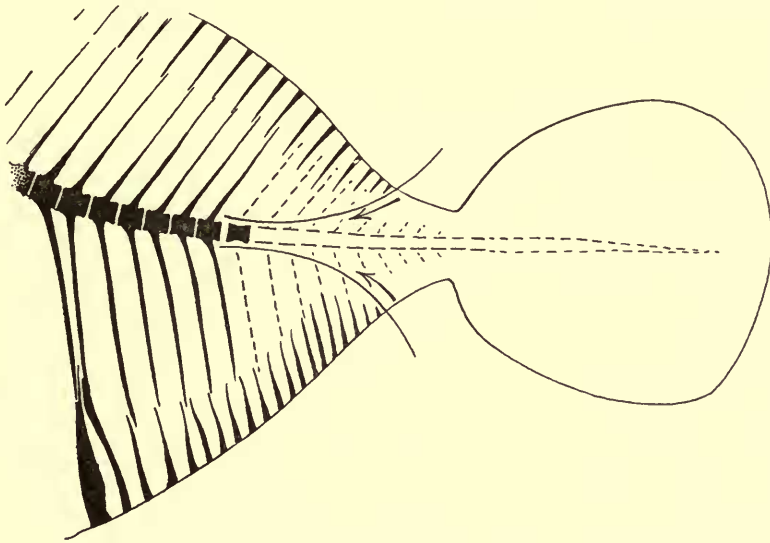

FIG. 1. Diagram illustrating reduction of the caudal region in the Molidae.

Persistent parts of the axial skeleton shown in black; atrophied parts shown with broken line; the last interneural and interhaemal bones close in along the lines marked with arrows. (Based on Ryder, 1886, modified by reference to adult and larval forms.)

there are only 12 caudal rays, exceptionally 13, and sometimes as few as 10. But in *Ranzania* and *Masturus* the clavus is supported by 20 or more rays, in *Mola ramsayi* by 16, and only in *Mola mola* by 12.

These rays are, in the main, supported by elements which have all the appearance of belonging to the series of interspinous supports of the dorsal and anal fins, but have been rotated to lie roughly at right angles to the last normal vertebro-interspinous complex by the process which has already been suggested by Ryder (Fig. 1). The skeletal supports of the clavus are accompanied by muscles which have split off from the inclinators of the dorsal and anal fins, and caudal muscles appear to have been lost with the posterior vertebral structures. Reduction of the caudal region can be shown to extend to the number of rays supporting the clavus. Thus in *Ranzania*, which has 18 remaining vertebrae, there are 22 rays of dorsal and anal origin in the clavus; in *Masturus* and *Mola*, which have 17 vertebrae, we find the series: *Masturus* 14–18 (exclusive of caudal rays), *Mola ramsayi* 16, *M. mola* 12.

Alongside this the form of the rays is of interest (see Barnard, 1935). In *Ranzania*

each ray in the clavus (except the outermost) is abruptly branched at its distal end (like those of the dorsal and anal lobes) and forms a fairly stiff fan-shaped support, closely apposed to those each side of it. In *Mola* this branched portion becomes hyperossified into a single plate or ossicle characteristic of the genus, the number and arrangement of these ossicles being of importance in specific diagnosis.

In *Masturus* the rays seem never to be branched in adults, and are never ossified distally, but in young examples they may be branched at the tip like those of *Ranzania*. This development can be seen by comparing the figures accompanying this paper. Between the rays in *Ranzania* lie elongate lobes of apparently collagenous material (shown in Fig. 3), and it is probably these which in *Mola mola* extend back between the widely spaced rays to form the lobes characteristic of the clavus of large specimens of that species.
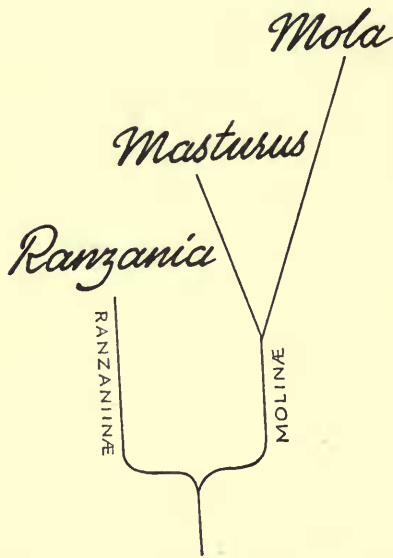
As a matter of interest, it may be remarked that *Ranzania*, *Mola*, and the Percomorphous family Carapidae (Fierasferidae) are the only fishes to which the term 'gephyrocercal' can properly be applied, as pointed out by Ryder when originally proposing the term.

Raven has taken the view that *Ranzania* is the most specialized of these genera. I cannot agree with this. Its skeleton is much less degenerate than that of *Mola*, more strongly ossified, and there are 18 or 19 vertebrae. The *lateralis* muscles are still moderately developed, though inserted posteriorly on the *m. dorsalis profundus*; the usual division of the dorsal portion into superior and inferior parts is still quite distinct anteriorly. I feel sure that Raven was mistaken in identifying the *lateralis* muscles as dorsal and anal depressors; they insert on to the latter but are distinct. The gill-rakers are free and apparently functional as in more generalized fishes. Further, this species is not gigantic.

FIG. 2. Relationships of the genera of the family Molidae.

It is not suggested, however, that *Ranzania* is completely representative of the ancestor of the other two genera; it has retained more primitive features, but it has completely lost the caudal fin, whereas *Masturus*, which is otherwise a stage farther towards *Mola*, retains a vestige of this fin, as will be shown later.

The relationships of these genera are therefore probably as shown in Fig. 2. An ancestral form in which the skeleton and musculature is still fairly normal and the caudal fin not completely lost gives rise to *Ranzania* on the one hand, which loses its caudal fin, and to *Masturus* on the other, in which the caudal fin retains a precarious hold but the skeleton and the musculature deteriorate. Further degeneration and complete loss of the caudal fin in this second line gives us *Mola*.

The need to recognize *Masturus* and *Mola* as more closely related to each other

than to *Ranzania* therefore still remains, and these two lines can now be expressed as subfamilies.

The three genera illustrate quite well the manner in which the *lateralis* muscles lose their primary function of flexing the body and become successively more closely associated with the dorsal and anal fins, their added power enabling these fins to
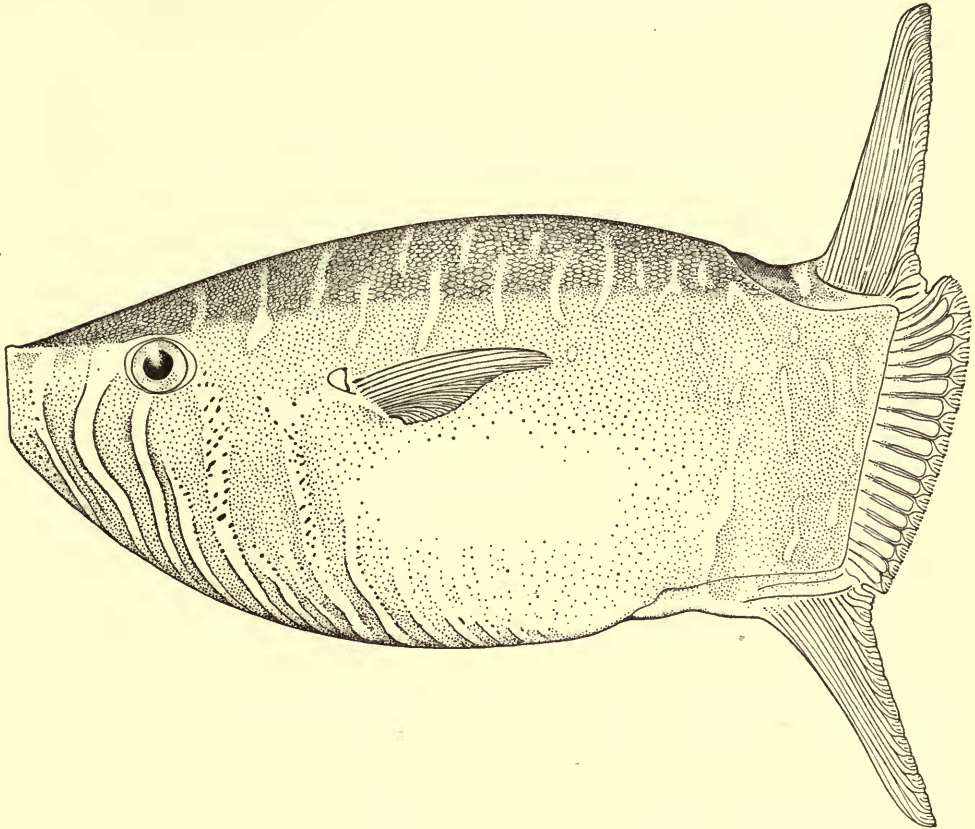
Fig. 3. *Ranzania laevis*, adult. A specimen 515 mm. long, from Baltimore, County Cork, Ireland.

become proportionately larger. The body is therefore held rigid, assisted in *Ranzania* by a carapace similar to that of *Strophiurichthys* among the Ostracionts, but with much smaller hexagonal plates; in *Masturus* and *Mola* this carapace is reduced to small denticles, and rigidity is assisted by a thick collagenous layer beneath the skin (Green, 1901).

All the species pass through a remarkable metamorphosis. The newly hatched larvae are *Tetraodon*-like, but soon (at 1–8 mm.) develop a cuirass of broad plates with jutting triangular projections, looking more reminiscent of an Ostraciont (Richardson named this stage *Ostracion boops*). With the atrophy of the larval tail, *Ranzania* seems to pass, by reduction of the cuirass and elongation of the body, into

a form essentially like that of the adult though proportionately longer, but *Masturus* and *Mola* show an intermediate stage, wherein the cuirass breaks up into small denticles and the triangular projections grow into long sharp spines on broad polygonal grooved bases (very like those of *Acanthostracion* or *Lactoria*). This stage is much shorter in the body than the adult. As growth proceeds the body lengthens and the spines shorten and disappear, though in *Mola* the bases of one on the snout and one at the chin are nearly always retained even in the largest specimens.

KEY TO THE GENERA OF MOLIDAE

I. Form comparatively elongate. Vertebrae 8+10 or 11. Carapace of smooth hexagonal plates,[1] terminating at bases of dorsal and anal fins and clavus. Lips produced forward beyond teeth as a funnel, closing as a vertical slit. Gill-rakers free. 2 uppermost branchiostegal rays coalesced. Clavus with 22 rays, all borne on interspinous bones. No secondary post-larval metamorphosis (subfamily RANZANIINAE) .   .   .   .   1. *Ranzania*

II. Form shorter. Vertebrae 9+8. Carapace collagenous; skin of body and clavus with small rough denticles. Lips not funnel-like. Gill-rakers concealed in thick skin. 6 distinct branchiostegal rays. A secondary post-larval metamorphosis (subfamily MOLINAE).

    A. Median rays of clavus not borne on interspinous bones, supporting a pronounced lobe; none of the rays bearing ossifications distally .   .   .   .   2. *Masturus*

    B. All rays in clavus borne on interspinous bones, most of them terminating in an ossification distally .   .   .   .   .   .   3. *Mola*

Genus *RANZANIA* Nardo

? *Triurus* Lacepède, 1800, *Hist. Nat. Poiss.* **2**: 200. Type: *Triurus bougainvillianus* Lacepède.
Ranzania Nardo, 1840, *Ann. Sci. Regno Lombardo-Veneto*, **5**: 10, 105. Type: *Ranzania typus* Nardo (= *Ostracion laevis* Pennant).
Centaurus Kaup, 1855, *Arch. Naturgesch.* **21** (1): 221. Type: *Ostracion boops* Richardson (= *Ostracion laevis* Pennant, young).

    The characters of this genus have been indicated concisely in the foregoing key.
    Lacepède's description of *Triurus bougainvillianus* was based upon manuscript notes by Commerson. It could be interpreted as referring to the fish later known as *Ranzania*, but to describe the funnel-like lips as 'rictu fistulari' or 'le museau avancé en forme de tube' and again 'un museau très prolongé fait en forme de tube assez étroit' requires a good stretch of imagination. Moreover, the depth of the body is given as the proportion of 18 against the body-length of 71, and no other Sunfish has been recorded as slender as that. Finally, it has to be noted that in vol. 1 of the same work *Ranzania* is figured (pl. 22) under the name 'le Tetrodon lune'. The status of the name *Triurus* is therefore doubtful, and I hesitate to follow Whitley in using it, particularly since the name *Ranzania* is so well known.
    A single species.

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[1] In young specimens (90 mm.) each plate has a prominent bony tubercle centrally.

Ranzania laevis (Pennant)

Ostracion laevis Pennant, 1776, *Brit. Zool.*, ed. 4, **3**: 129, pl. 19.

Tetrodon truncatus Retzius, 1785, *K. Svenska Vetensk Akad. Handl.* **6** (2): 121 (based on Pennant) ;
  Lacepède, 1798, *Hist. Nat. Poiss.* **1**: 514, pl. 22 f. 2 ; Donovan, 1808, *Nat. Hist. Brit. Fish.*
  2: pl. 41.

Orthagoriscus oblongus Bloch & Schneider, 1801, *Syst. Ichth.*: 511, pl. xcviii.

Orthagoriscus oblongus Jenyns, 1835, *Man. Brit. Vertebr. Anim.*: 491 ; Yarrell, 1836, *Hist. Brit.*
  Fish. **2**: 357, fig. ; Couch, 1841, *Ann. Mag. Nat. Hist.* **6**: 144 ; Bonaparte, 1846, *Cat. Met.*
  Pesci eur.: 88 ; Bleeker, 1860, *Natuurk. Tijdschr. Ned.-Ind.* **21**: 57 ; Couch, 1865, *Hist. Fish.*
  Brit. Is. **4**: 381, pl. 246 ; Harting, 1868, *Verh. Akad. Wet. Amst.*: 12, pl. 2, fig. 2 ; Andrews, 1871,
  Proc. Nat. Hist. Soc. Dublin, **5**: 123 ; Sauvage, 1891, *Hist. Madagascar*, **16** (Poiss.): 529 ;
  Nobre, 1935, *Faun. Mar. Portugal, Vertebr.*: 242.

Cephalus oblongus Shaw, 1806, *Gen. Zool.* **5**: 439, pl. 176 ; Swainson, 1839, *Nat. Hist. Class. Fish.*
  2: 330.

Cephalus varius Shaw, 1806, ibid.

Orthragus commersoni Rafinesque, 1810, *Caratt. Sicilia*: 18.

Orthragus oblongus Rafinesque, 1810, *Indice Itt. Sicil.*: 40.

Tetraodon truncatus Couch, 1825, *Trans. Linn. Soc. Lond.* **14**: 88.

Cephalus elongatus Risso, 1826, *Eur. Mérid.* **3**: 173.

Mola planci Nardo, 1828, *Bull. Sci. Nat. Férussac*, **13**: 437.

Orthagoriscus truncatus Fleming, 1828, *Hist. Brit. Anim.*: 175 ; Günther, 1870, *Cat. Fish. Brit.*
  Mus. **8**: 319 ; Bleeker, 1873, *Ned. Tijdschr. Dierk.* **4**: 121 ; 1879, *Verh. Akad. Wed. Amst.* **18**: 26 ;
  Rochebrune, 1883–1885, *Faune Sénégambie* (Poiss.): 157 ; Day, 1884, *Fish. Gt. Brit.*: 276,
  pl. 149 ; Beauregard, 1893, *Bull. Soc. Sci. Nat. Ouest*, **3**: 229 ; Scharff, 1906, *Irish Nat.* **15**: 275 ;
  Mauro, 1906, *Boll. Accad. Gioenia, Catania*, N.S. **85**: 16, fig.

Cephalus cocherani Traill, 1832, *Mem. Werner*: **6**.

Orthagoriscus elegans Ranzani, 1839, *Novi Comment. Acad. Sci. Inst. Bonon.* **3**: table.

Orthragoriscus battarae Ranzani, 1839, ibid.

Ranzania typus Nardo, 1840, *Ann. Sci. Regno Lombardo-Veneto*, **5**: 105 ; Smith, 1949, *Sea Fish.*
  S. Afr.: 422, pl. 95, fig. 1212.

Ostracion boops Richardson, 1844, *Voy. Erebus and Terror, Fish.*: 52, pl. 30, figs. 18–21 ; Günther,
  1880, *Intro. Study Fish.*: 175, fig. 93.

Orthagoriscus planci Bonaparte, 1846, *Cat. Met. pesci eur.*: 88 ; Canestrini, 1872, *Fauna d'Italia*,
  Pesci: 149 ; Stossich, 1879, *Boll. Soc. Adriat. Sci. Nat.* **5**: 36.

Orthragoriscus lunaris (Gronow) Gray, 1854, *Cat. Fish.*: 165.

Centaurus boops Kaup, 1855, *Arch. Naturgesch.* **21** (1): 221.

Ranzania truncata Jordan & Gilbert, 1883, *Bull. U.S. Nat. Mus.* **16**: 966 ; Trois, 1884, *Atti Ist.*
  Veneto, **2** (6) pt. 1: 1269, pls. 12–14 ; pt. 2: 1543, pl. 16 ; Perugia, 1897, *Ann. Mus. Stor. nat.*
  Genova (2), **18**: 140 ; Jordan & Evermann, 1898, *Bull. U.S. Nat. Mus.*: **47** (2): 1755 ; Steenstrup
  & Lütken, 1898, *K. danske vidensk. Selsk. Skr.* (6) **9**: 54, fig. ; Günther, 1910, *J. Mus. Godeffroy*,
  9 (17): 477 ; Pellegrin, 1912, *Bull. Soc. Zool. France*, **37**: 228, fig. 1 ; Ribeiro, 1915, *Arch. Mus.*
  nac. Rio de J. **17** (Molidae): 4, pl. ; Thompson, 1918, *Mar. Biol. Rep. Cape Town* **4**: 176 ; Buen,
  1919, *Bol. Pesc. Madr.* **4**: 295 ; 1935, *Notas Inst. esp. Oceanogr.* **2** (81): 146 ; Schmidt, 1921,
  Nature, Lond. **107**: 76, figs. 2, 4, 5 ; *Medd. Komm. Havundersøg. Fisk.* **6** (6), fig. 2. 13, pl. 1,
  fig. 7 ; Fowler, 1922, *Copeia* **112**: 84 ; Vinciguerra, 1923, *Comune di Genova* **3**: 5, fig. 3 ; Barnard,
  1927, *Ann. S. Afr. Mus.* **21**: 989, fig. 32 ; Fowler, 1928, *Mem. Bishop Mus.* **10**: 475 ; Schmidt,
  1932, *Dana's Togt omkr. Jord.*: 251, fig. 197 (6–11) ; Gudger, 1935, *Nature, Lond.* **135**: 548 ;
  Barnard, 1935, *Ann. S. Afr. Mus.* **30**: 655, fig. 6 c ; Ehrenbaum, 1936, *Handb. Seefisch. Nord-*
  europ. **2**: 88, fig. 69 ; Gudger, 1936, *Nature, Lond.* **137**: 947 ; Fowler, 1936, *Bull. Amer. Mus.*
  Nat. Hist. **70** (2): 1123, fig. 470 ; Ninni, 1939, *Atti. Soc. Ital. Sci. nat.* **78**: 236 ; Raven, 1939,
  Amer. Mus. Novit. **1038**, figs. 1–3 ; Clark, 1949, ibid. **1397**: 7, fig. 9 ; Maul, 1949, *Vertebr.*
  Madeira **2** (Peixes): 158.

Ranzania makua Jenkins, 1895, *Proc. Calif. Acad. Sci.* (2) **5**: 780, pl. ; Fowler, 1900, *Proc. Acad.*

Nat. Sci. Philad.: 514; Jordan & Snyder, 1901, *Proc. U.S. Nat. Mus.* **24**: 262; Jenkins, 1902,
Bull. U.S. Fish. Comm. **22**: 486 (1903); Jordan & Evermann, 1905, *Bull. U.S. Fish. Comm.*
23 (1): 439, fig. 194; Jordan, Tanaka, & Snyder, 1913, *J. Coll. Sci. Tokyo* **33**: 231, fig. 166;
Snyder, 1913, *Proc. U.S. Nat. Mus.* **44**: 460, pl. 63; Tanaka, 1914, *Fig. Descr. Fish. Japan*
16: 274, pl. 76; Jordan & Jordan, 1922, *Mem. Carneg. Mus.* **10** (1): 89; Jordan, Evermann, &
Tanaka, 1927, *Proc. Calif. Acad. Sci.* **16** (4): 680.
Orthagoriscus (larva) Sanzo, 1919, *Mem. R. Com. Talassogr. ital.* **69**: 1–7, figs. 1–4.
Ranzania laevis Whitley, 1933, *Vict. Nat.* **49**: 211, figs. 6, 7; Phillips, 1941, *Trans. Proc. Roy. Soc.
N.Z.* **71** (3): 245, pl. 41, fig. 6; Deraniyagala, 1944, *J. Bombay Nat. Hist. Soc.* **44** (3): 429.
Triurus laevis Whitley, 1937, *Mem. Queensland Mus.* **11** (2): 147; Hale, 1944, *S. Aust. Nat.* **22**:
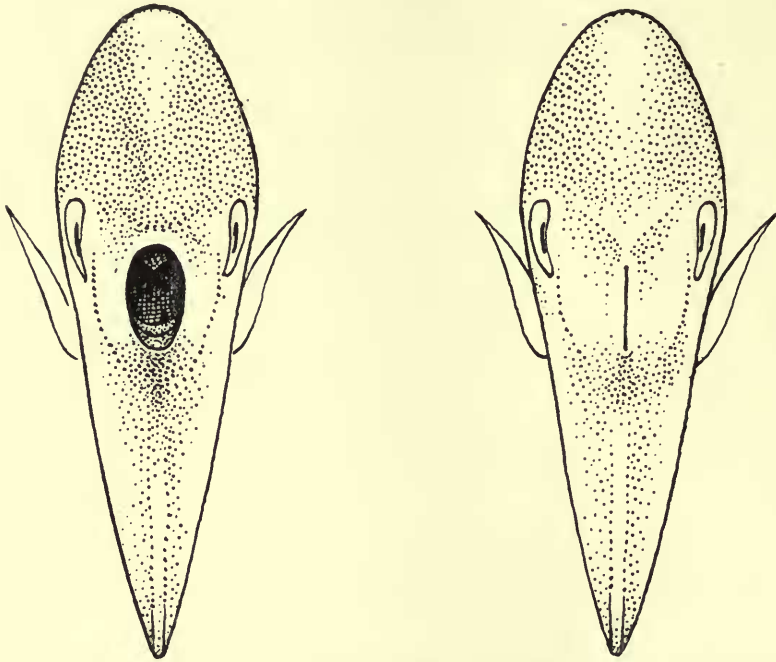pt. 4, pl. 1, figs.

FIG. 4. *Ranzania laevis*. Front view of head, showing mouth open and closed.

Examination of the records leaves little doubt that a single species of *Ranzania* ranges the seas of the whole world except the polar regions, but it seems that two subspecies can be recognized as follows:

Ranzania laevis laevis (Pennant). Depth of carapace contained twice or more in its length, in adults (up to 580 mm.). Axil of pectoral fin well below level of centre of eye. Height of anal fin less than $\frac{3}{5}$ length of head. Atlantic Ocean.

R. 1. makua Jenkins. Depth of carapace contained less than twice in its length, in adults (400–500 mm.). Axil of pectoral fin above level of centre of eye. Height of anal fin $\frac{2}{3}$ length of head or more. North Pacific Ocean.

That these two forms are simply subspecific extremes in the range is shown by the records from the Indian Ocean, wherein the depth is usually given as for *makua* while

the pectoral fin is low as in *laevis*. A specimen from Mauritius in our collection shows these features well, and a closely similar specimen has been figured by Whitley from Australia.

Whenever the coloration has been described it has been shown to be closely similar in all these forms, a pattern of pale transverse bands on a darker ground, the bands edged with spots and broken lines of black; three bands associated with the eye are
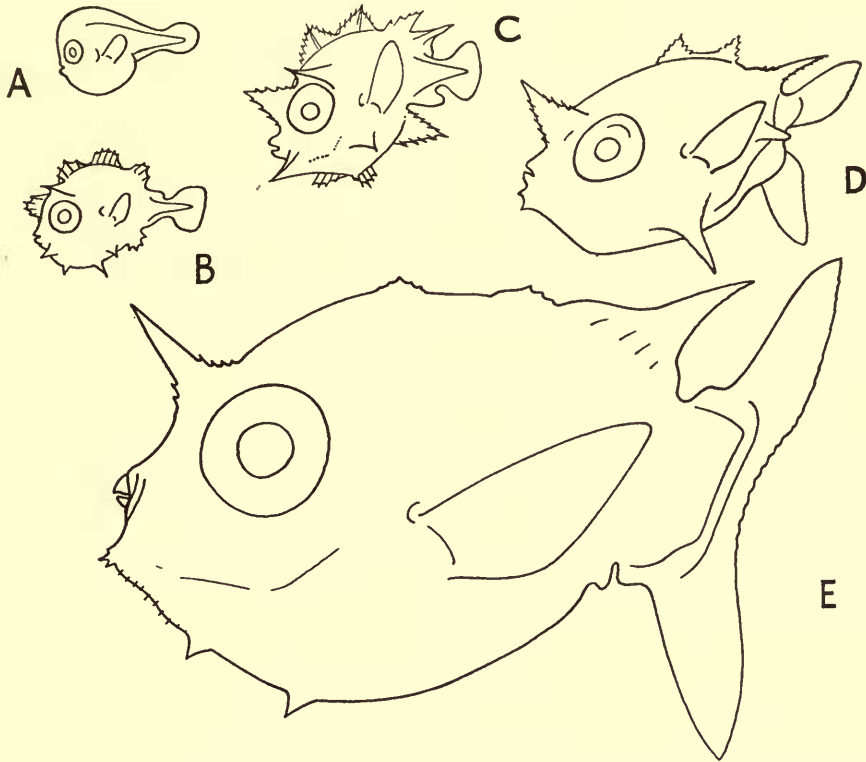

FIG. 5. Development of *Ranzania laevis*.
A, larva (1·7 mm.); B, C, D, early, full, and late '*Ostracion boops*' stage; E, transition to adult form (8 mm.). (After Schmidt.)

the most constant, the posterior ones being variously broken or anastomosed, sometimes enclosing large oval areas of the ground colour. The colours are said to be very brilliant in life.

The mouth is very curious, the lips extending well beyond the teeth and forming a funnel, the mouth being oval with the long axis vertical. The orifice closes along this axis, so that the rictus is really vertical—apparently unique among fishes (Fig. 4). This feature was shown clearly in the earliest published picture of the fish (Aldrovandi, 1613), a remarkably good representation for its period.

Too little is known of the feeding habits to show whether they can be associated with the peculiar mouth, but the species has been reported to take littoral algae

(Barnard, 1927), and it is possible that the lips can suck in and close upon a frond while the teeth nip it off.

The fine developmental series given by Schmidt (1932) shows that Raven was correct in supposing that elongation of the body is secondary, but it also shows that *Ranzania* is never so greatly shortened as the other two genera (Fig. 5). Lengthening occurs after the 8-mm. stage, until at 53 mm. the length of the carapace is about 3 times its depth. This proportion is maintained up to 90-mm. size, and after that the depth of the body increases with growth, so that at 250 mm. the length of the carapace is 2·5 times its depth, at 430 mm. 2·25 times, at 515 mm. 2·1 times, and at 580 mm. only twice. These figures are for the Atlantic form as shown by our specimens; in the North Pacific subspecies *R. makua* either the early lengthening is not so great or the later deepening is more rapid.

The general use of the name *truncatus* for this species seems to date from Günther, 1870; it is not clear why he chose this name rather than that of Pennant, on whose work that of Retzius was based, but possibly it was due to the fact that Pennant's description was numbered 54, while on his plate the number 54 appears beside a figure of the 'Short Diodon' (*Mola mola*), leaving the other Sunfish without a number. As both description and figure are titled 'Oblong Diodon', however, this is clearly an error in numbering, and there can be no doubt as to the identity of *Ostracion laevis*, which antedates *Tetrodon truncatus* by nine years.

Ranzania laevis does not reach so enormous a size as the other members of the family, apparently not exceeding 800 mm. in length. It has been recorded from all warm seas, as far north as Scandinavia and far south as New Zealand, usually from single specimens—though it was once observed in great numbers at the surface of the water off Martinique (Pellegrin, 1912). As Schmidt has pointed out, most records of larval Sunfishes to date belong to this species, and he has given us a fairly complete picture of its development from egg to adult.

Genus *MASTURUS* Gill

Masturus Gill, 1884, *Proc. U.S. Nat. Mus.* **7**: 425. Type: *Orthagoriscus oxyuropterus* Bleeker.

The study of this genus has been greatly facilitated by the careful bibliographical work of Gudger, who studied the records over a number of years, added several new ones, and finally in 1937 published a work dealing with the structure of the caudal region and another summarizing the knowledge of the genus up to that date. The latter two works are of great value, and the remarks which I make in the pages which follow are based largely upon them and should be considered with constant reference to them.

The distinctness of *Masturus* from *Mola* had already been acknowledged by Steenstrup & Lütken (1898), and discrimination between the post-larval forms was achieved by Schmidt (1921). The secondary post-larval stage of *Masturus* is characterized by enormous elongation of the 'cornicles' (Fig. 6). But it remained for Gudger to disentangle the confusion in the literature, and it is no doubt because these necessitated a chronological arrangement of his data that he was unable to recognize the two forms involved. But an analysis of the records leaves little room for doubt that there

are indeed two forms, one the generally accepted *M. lanceolatus* (Liénard), the other apparently taking *M. oxyuropterus* (Bleeker) as the earliest name. These will be diagnosed on a later page, but it is necessary to note their existence at this point in order to clarify the discussion which follows. I must stress now, however, that they are regarded here as species only because we have no knowledge to the contrary, but I suspect that they may prove to be the sexes of one species. Not one of the
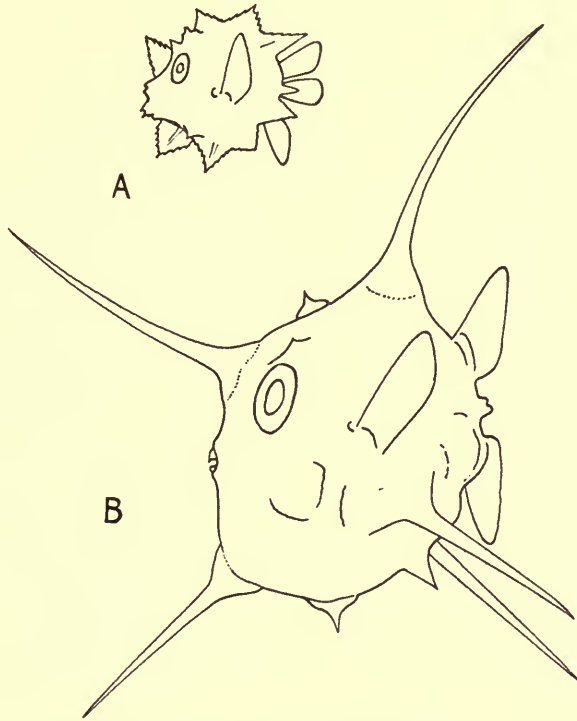

FIG. 6. Post-larvae of *Masturus*.
A, '*Ostracion boops*' stage (2·8 mm.); B, '*Molacanthus*' stage
(5 mm.). (After Schmidt.)

specimens so far recorded has been sexed. Raven, the only person to make a dissection, does not even mention the gonads.

Masturus is peculiar among the Molidae in the possession of a pronounced lobe a little above the centre of the clavus. Gudger continually stressed the dorsal situation of this lobe, apparently as evidence that it could not be the remains of the larval tail; this is not a very good point, for his own anatomical figures show that the lobe is associated with the end of the vertebral column. In other Plectognathi the vertebral column lies dorsally until it enters the caudal peduncle, where it lies approximately in the central long axis of the body. The fact that in the Molidae the vertebral column is dorsally placed at its hind end is therefore interesting as a further demonstration that the posterior part of the column is lost.

It is my belief that the lobe on the clavus of *Masturus* can truly be called the

'caudal lobe', for all the illustrations of its anatomy so far given seem to demonstrate that the slender rays supporting it are caudal rays. The first to be published was that by Ryder, after a drawing by Putnam; it was reproduced by Gudger, and is now copied as my Fig. 7 A. It is interesting in that the dorsal and anal rays of the clavus are shown branched, a feature shown only once elsewhere in the literature (Gudger, 1939), perhaps because the tips are so often broken off in young specimens. They are
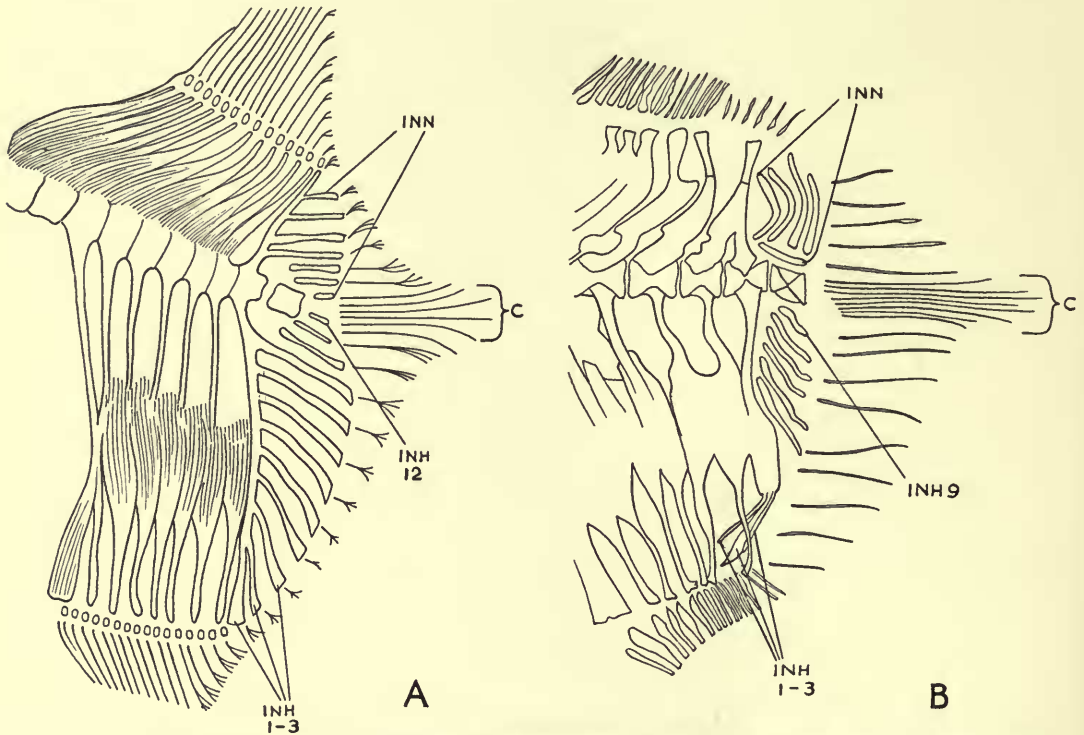

FIG. 7. Caudal skeletons of A, *Masturus oxyuropterus*, copied from Ryder, 1886; B, *Masturus lanceolatus*, copied from Gudger, 1937.

c, caudal rays; INN, interneural bones; INH, interhaemal bones.

thus distinguishable at a glance from the simple caudal rays in the middle, but it is probable that the outermost two of the latter are also of dorsal and anal origin, for they have each a small skeletal support.

The interspinous bones supporting the clavus are shown completely fused with the hindmost remaining haemal spine. Comparison with other dissections shows that these must in fact have been distinct elements. The shape of the supporting bones of the dorsal and anal fin lobes is obscured by the inclinator muscles in this figure, but the drawing of these muscles is interesting in helping to show their character after the *lateralis* mass has been removed.

Each of the rays in the clavus is supported by an interspinous bone, with the exception of the middle four; these are associated with the last of the remaining vertebrae,

which has no neural or haemal elements. There is no apparent reason why, if they also are dorsal and anal rays, they should not have their supports; but if they are caudal rays they cannot be expected to be borne on hypurals, since these and other posterior vertebral elements have been lost. The presence of only four of these unsupported rays and the equal length of the dorsal and anal fin bases shows that Putnam's fish was a *Masturus oxyuropterus*; two other dissections of this form have been illustrated—that by Gudger (1937 *a*, p. 41, fig. 27), and that by Raven (1939 *b*). The first does not show the internal skeleton, and one of the caudal rays is doubled, as can be seen by the nature of its basal cartilage; but Raven's illustration, drawn by Helen Ziska, is admirable, and agrees in all essentials with that by Putnam. The only illustration showing the anatomy of *M. lanceolatus* is that given by Gudger in the work just quoted, based upon a young specimen (the same size as Putnam's) which was stained with alizarin and cleared. During the staining process some of the elements, notably the interneural supports of the clavus, were displaced, but I am satisfied that nothing was lost. This illustration is copied here as my Fig. 7 B. Here it will be seen that the central lobe of the clavus is supported by eight rays whose only skeletal support is the last vertebra (which has no neural or haemal elements). Above these are five rays which can be associated with the five interneural bones which have been displaced from the horizontal during preparation. Below them are nine rays which belong to nine interhaemals, the lower three of which have been displaced forward. The presence of eight rays in the caudal lobe of the clavus and the greater length of the base of the dorsal fin lobe as compared with that of the anal fin lobe shows this to have been a specimen of *Masturus lanceolatus* as identified by Klunzinger (a figure of whose specimen is given by Gudger).

It is admittedly hazardous to speak of caudal rays when the hypural bones are lost, since in normal fishes caudal rays are distinguishable only by their association with the hypurals. But I feel convinced that these central rays of the clavus in *Masturus* are homologous with the hypocaudal rays of the more generalized forms, and it remains for me to suggest how it is possible for them to persist although their skeletal supports are lost.

It has to be borne in mind that two opposing forces are involved during the development of the caudal region, interacting in different proportion at successive stages. First there is the reduction of the larval tail and the atrophy of the posterior vertebral elements, and secondly the normal growth of body and fins.

The first process evidently begins at an early age, for Schmidt has figured a larval specimen in which, as Gudger has pointed out, dorsal and anal rays are present but not caudal rays; development of the latter is retarded. To see how this fact may affect later stages it is necessary to consider what occurs in the Triacanthodidae, the most primitive family of Plectognathi. In the larval Triacanthodid (Fig. 8), the caudal rays are twelve in number, as in most Plectognathi, but the last four lie in relation to the end of the notochord, which will later become ossified as the urostyle; the anterior eight belong to the last few myotomes. Degeneration of the tail from the rear will mean that the end of the notochord is lost first, and if this occurs before the hypocaudal rays appear not more than eight of them will develop. The eight slender rays of *Masturus lanceolatus* thus become intelligible and significant, while the

presence of only four in *M. oxyuropterus* suggests that reduction has proceeded still farther before caudal rays begin to develop in this form. Comparison with the larval *Mola* figured by Sanzo (1939) is interesting in this connexion, for it will be seen that if in his specimen hypocaudal rays were developed, they would not be associated with myotomes, and this probably accounts for their absence in that genus.

As the caudal rays become stronger the axial structures decrease rapidly, so that by the time the rays are brought to the homocercal position there are no hypurals for their support, nor neural or haemal elements for the last few vertebrae; but normal
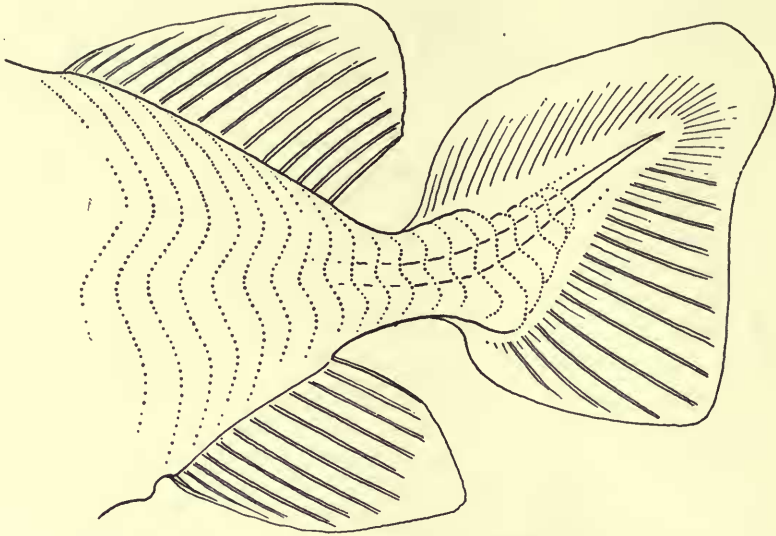

FIG. 8. Caudal region of post-larval Triacanthodid fish, showing relationship of hypocaudal rays to notochord and myotomes.

body growth has extended the posterior parts of the dorsal and anal fins with their supporting structures backward and downward to fill the void. This process is probably correctly demonstrated by Ryder's diagram, upon which mine is based (Fig. 1), in which the region of atrophy is delineated by the broken line. The vertebrae with their neural and haemal arches and spines are lost, but the interneural and interhaemal spines develop in relation to the fins in the normal manner except that they ultimately become tilted nearly at right angles to the last developed vertebral elements (Fig. 7). The number of these interspinous bones does not give a reliable estimate of the number of vertebrae that have been lost, because reference to the dissections shows that more than one may be associated with each neural or haemal spine, while of course the last few vertebrae are probably not associated with interspinous bones at all. Ryder, of course, thought Putnam's young fish was a *Mola* and that the caudal rays were completely lost in the adult. A curious feature of the posterior migration of the dorsal and anal fins is that, while in the lobes the rays are more numerous than the interspinous bones, each of those in the clavus has its own supporting element; this might be taken to indicate that the central rays, which I

regard as caudal, are simply the last dorsal and anal rays, which are therefore more numerous than their supports in this region also, but there seems no good reason why the odd rays should all be crowded at the end. A more difficult argument to combat is that the supporting elements of these last rays cannot develop because of the presence of the vertebral column; against this I can only point out that in Putnam's fish two elements lie *behind* the last vertebra, and there seems no reason why, if the odd four rays were in the same series, their supporting bones should not be there also. In fact, the presence of the two elements mentioned is reminiscent of the condition
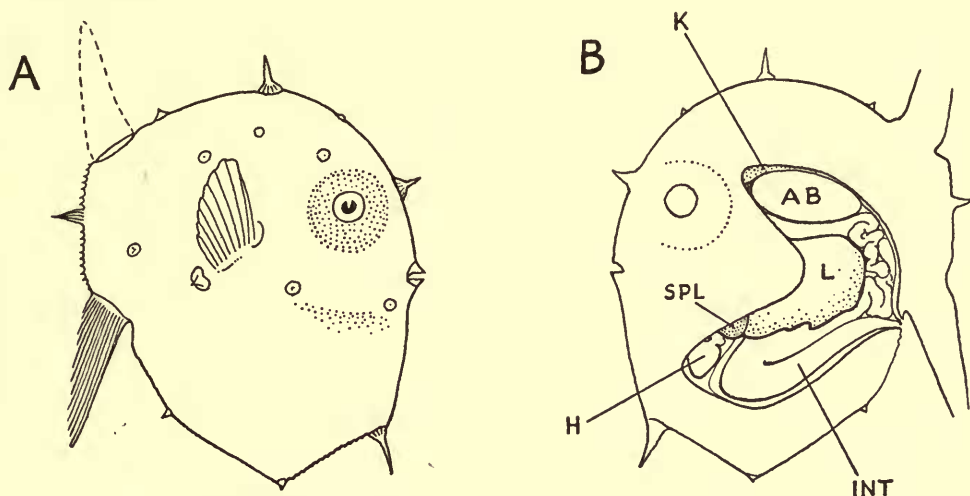

Fig. 9. *Masturus oxyuropterus*, late post-larva (21 mm.), in British Museum collection. B, dissection of same specimen, showing presence of air-bladder.
AB, air-bladder; H, heart; K, kidney; L, liver; INT, intestine; SPL, spleen.

shown in *Cyema atrum* by Trewavas (1933), who identified the two small ossifications as hypurals. But since the last caudal vertebrae are so obviously lost in the Molidae it would be incautious to speak of hypurals here.

McCulloch has left us drawings of very young examples of both *M. lanceolatus* and *M. oxyuropterus*, at the stage when the larval tail is not quite lost, the small peduncle bearing its allotted quota of caudal rays and the dorsal and anal fins extending round to meet them. Knowing what a careful observer and excellent draughtsman McCulloch was, I am prepared to accept these as good evidence. Eventually, at the better known stage of 50 mm. or thereabouts, there is no sign of the original tail, but the caudal rays project beyond the rest of the clavus as the basis for the ultimate central lobe. Gudger believed that even these central rays were lost, at what he called the 'square-tailed' stage, but as this was based on the two obviously damaged specimens of Steenstrup & Lütken, this seems to be improbable—a point which Dr. Gudger himself has conceded in a letter to me.

As a matter of interest I may mention here that in these small specimens it appears that the air-bladder is still present; one which I dissected (Fig. 9 B) had a very

delicate, bubble-like structure at the centre of mass, which unfortunately collapsed while I was examining it. At this planktonic stage in its development such an organ is not surprising, and of course the Molidae are evolved from fishes in which the air-bladder is well developed, but it is worth noting that the statement that an air-vessel is absent in this family is probably true only of adults.
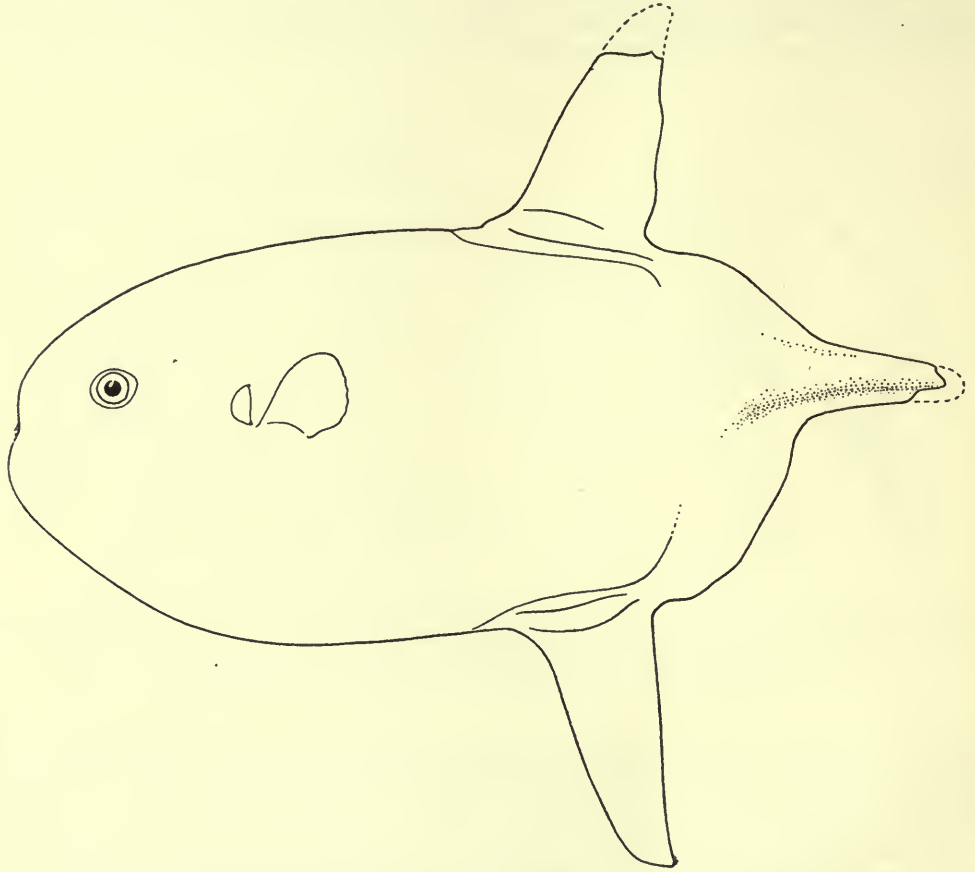

FIG. 10. *Masturus lanceolatus*, adult. Singapore. (After Smedley, 1932.)

With the development of the skeletal structures (poorly ossified though they are) atrophy proceeds no farther, and the processes of growth produce what later changes we can observe in the fish. An extension of the dermis and its collagenous sub-stratum, probably that which would develop over the caudal peduncle in a more normal fish, eventually covers the caudal lobe and the whole clavus.

These are what seem to be the main features in the development of the clavus of *Masturus*, but there is a certain amount of individual variation. In *M. lanceolatus* the presence of eight caudal rays seems to be fairly consistent, but the middle ones are sometimes represented only distally—whether their proximal ends atrophy in the early stages or degenerate later is not evident. In *M. oxyuropterus* four caudal rays

are usual, but may occasionally be five (as in a dissection figured by Gudger, wherein one of the rays had split or doubled as shown by its supporting cartilage) or rarely three. On published evidence the number of rays supporting dorsal fin, clavus, and anal fin respectively appear to differ very greatly, but most of these are of doubtful value, for an accurate count can only be made by dissection (except possibly in stuffed specimens). As an example of this may be quoted the description by Gudger, a careful worker, of the specimen he obtained for the American Museum of Natural History. In this he counted, on external examination, 'D.+C.+A. complex = 60'; the fish is in other respects *M. oxyuropterus*, so that this high count would cast doubt on its distinctness from *M. lanceolatus*. But later Raven dissected this same fish, and his illustration shows distinctly the total of fifty-five rays which is usual in *M. oxyuropterus*. Consequently it has not seemed expedient to give any definite statement of the number of rays to be found in dorsal and anal fins and clavus respectively, but only to indicate the total number, which seems to be characteristic for each species.

Whether or not I am correct in calling them caudal rays, the presence of median rays unsupported by interspinous bones is characteristic of *Masturus*. In the adults all the rays of the clavus are simple, without distal ossifications. There is always a median projection to the clavus, and the body is rather more elongate than that of *Mola*, especially in the early stages. Osseous tubercles, the remains of post-larval spines, seem never to be retained anywhere on the body of the adult.

Two forms can be recognized, treated here as species, but I suspect that further study will show them to be the sexes of one. They have been taken in the same localities, and sometimes together. The sexual dimorphism found to be present in *Mola mola* (p. 117) lends support to this idea. But with no knowledge of the sex of any recorded individual I can but state their characteristics and apply available names to them pending further information.

Since all the literature before 1939 has been fully quoted and discussed by Gudger, I have not thought it necessary to repeat it all below, particularly as a number of records cannot be assigned with certainty, but full and discriminating reference has been made to Gudger's papers.

KEY TO THE SPECIES OF *MASTURUS*

I. Profile of lower jaw more convex, usually projecting beyond the upper. Upper profile of head evenly convex. Base of dorsal lobe conspicuously longer than that of anal fin. Dorsal and anal fins and clavus with a total of 60 to 62 rays. Caudal lobe of clavus[1] longer than head in perfect specimens (often mutilated), supported by eight (rarely 7 or 9) rays . . . . . 1. *lanceolatus*

II. Profile of lower jaw less convex, straight or concave, not projecting beyond the upper. Upper profile of head with distinct concavity above the eyes. Bases of dorsal and anal fin lobes about equal. Dorsal and anal fins and clavus with a total of 55 to 57 rays. Caudal lobe of clavus shorter than head, supported by 4 (rarely 3 or 5) rays . . . . 2. *oxyuropterus*

The uncertainty of authors as to where dorsal and anal fins end and clavus begins,

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[1] Measured from 'hinge' of clavus to tip.

and the obvious inaccuracy (already mentioned) of fin-ray counts made upon external examination, militates against giving counts for individual fins, but it may be, as suggested by Gudger's cleared specimen, that in *M. lanceolatus* there are more
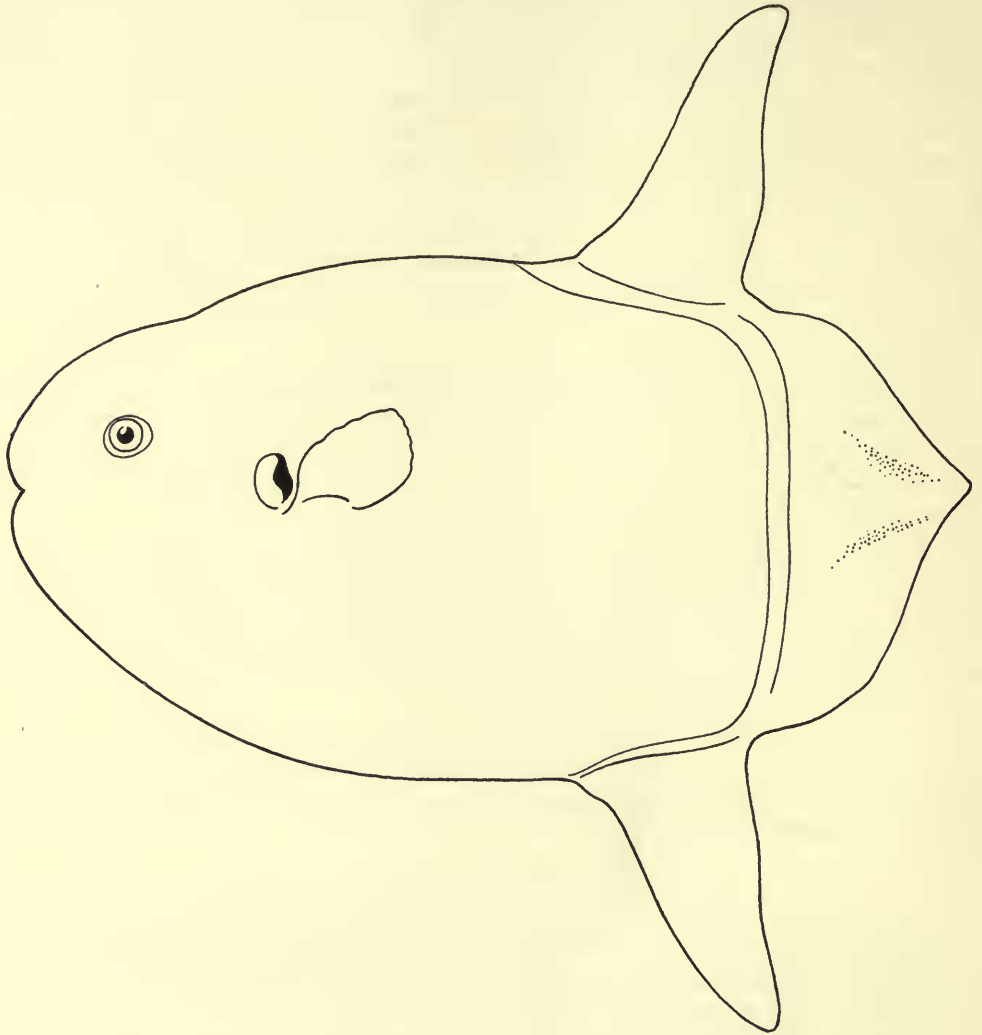

FIG. 11. *Masturus oxyuropterus*, adult. Tahiti. (After Gudger, 1935.)

rays in the dorsal lobe than in *M. oxyuropterus*. In the latter, on the other hand, the number of claval rays supported on interhaemal bones seems to be greater (10 to 12) than in *M. lanceolatus* (9).

Although usually these types seem to be recognizable at an early age, there are some doubtful cases among young specimens, as might be expected if they were the

sexes of one species. For example, if *M. lanceolatus* should be the male, it might be more like the female (*M. oxyuropterus*) when young, as in many other fishes, and in fact small examples of the *oxyuropterus* type seem to be the more common.

Masturus lanceolatus (Liénard)

Orthagoriscus lanceolatus Liénard, 1840, *Revue Zool.*: 291; 1841, *Magasin Zool.* (2) **3** (Poiss.): pl. 4.
Orthagoriscus mola Klunzinger, 1871, *Verh. Zool.-Bot. Ges. Wien*, **21**: 648; Günther, 1880, *Introd. Stud. Fish.*: 175, fig. 94; Perugia, 1881, *Ann. Mus. Stor. Nat. Genova* **27**: 365, fig.
Mola mola Collett, 1896, *Résult. Camp. Sci. Monaco* **10**: 163, pl. 6, fig. 1.
Ranzania truncata Steenstrup & Lütken, 1898, *K. danske vidensk. Selsk. Skr.* (6) **9**: pl. 6, fig. C. (Not of Jordan & Gilbert, 1883.)
Mola (Molacanthus) sp. McCulloch, 1912, *Proc. Linn. Soc. N.S.W.* **37** (3): 553, pl. 58.
Mola lanceolata Schmidt, 1921, *Medd. Komm. Havundersøg. Kbh., Fisk.* **6** (6): pl. 1, figs. 4, 5; 1932, *Dana's Togt omkr. Jord.*: 255, fig. 167 (*part.*); Barnard, 1927, *Ann. S. Afr. Mus.* **21**: 987, fig. 31; Ehrenbaum, 1936, *Handb. Seefisch. Nordeurop.* **2**: 88; J. L. B. Smith, *Sea Fish. S. Afr.*: 422, fig. 1214.
Masturus lanceolatus Hubbs & Giovannoli, 1931, *Copeia*, **1931**: 135; Gudger, 1935, *Amer. Mus. Novit.* **778**: 1, fig. 1; Gudger & McDonald, 1935, *Sci. Mon.* **41**: 1, figs. 4–9, 11, 14, 15; Rivero, 1936, *Amer. Nat.* **70**: 92, fig.; Palmer, 1936, *Science*, **83**: 597; Gudger, 1937, *Ann. Mag. Nat. Hist.* (10) **19**: 9, fig. 6; 15, fig. 10; 31, fig. 19; 33, fig. 20; 34, fig. 21; 38, fig. 23; *Proc. Zool. Soc. Lond.* **107** (A) (3): 353 (*part.*), text-figs. 1, 2, 4, 6, 7, 8, 9, 14 (?), 16, 20, 21 (?); pl. 1, figs. 3, 4; pl. 2, figs. 5, 6; pl. 4, fig. 10; 1939, *J. Elisha Mitchell Sci. Soc.* **55** (2): 305; Brimley, 1939, ibid. 295, pl. 28; Fitch, 1950, *Calif. Fish Game*, **36** (2): 65.

Liénard's figure cannot be said to be notable for its faithful representation, but as it shows the caudal lobe indubitably much longer than the head and the base of the dorsal fin longer than that of the anal, it shows to which of our two forms the name is applicable. The fin-rays are always more easily seen in dried specimens of these fishes, and so Klunzinger's stuffed example shows the structure of the clavus very well; it is closely similar (in this 65-in. example) to that of Gudger's 53-mm. cleared specimen. Other figures in Gudger's papers which appear to represent this form are stated in the above synonymy. Where the caudal lobe is mutilated or otherwise doubtful the broad dorsal base and rather pugnacious-looking 'chin' are the most useful distinguishing characters.

It grows to a great size, the largest recorded specimen being 10 ft. long and 11 ft. 3 in. from the tip of dorsal to tip of anal fins. In our collection it is represented only by the post-larval specimen figured by Günther.

Recognizable records of adults are from the Atlantic, off Florida, Havana, North Carolina, and Table Bay, South Africa, from the Red Sea, and from the Pacific at Tahiti. Young specimens have been taken off Alabama, Teneriffe, and in the South Seas. As this paper goes to press Fitch (1950) states that 100 post-larvae ¼ to 2 in. in length have been taken from the stomachs of tuna in Hawaiian waters.

Masturus oxyuropterus (Bleeker)

Orthagoriscus spinosus Gatchet, 1832, *Act. Soc. Linn. Bordeaux* **5**: 253. (Not of Cuvier, 1817.)
Orthagoriscus oxyuropterus Bleeker, 1873, *Versl. Akad. Amst.* (2) **7**: 151, fig.

Mola rotunda Ryder, 1886, *Rep. U.S. Fish. Comm.* (1884): 1027, pl. 8, fig. 5. (Not of Cuvier, 1798.)

Ranzania truncata Steenstrup & Lütken, 1898, *K. danske vidensk. Selsk. Skr.* (6) **9** (1): 98, pl. 6, figs. D, E. (Not of Jordan & Gilbert, 1883.)

Mola (Molacanthus) sp. McCulloch, 1912, *Proc. Linn. Soc. N.S.W.* **38** (3): 553 (*part.*), pl. 59.
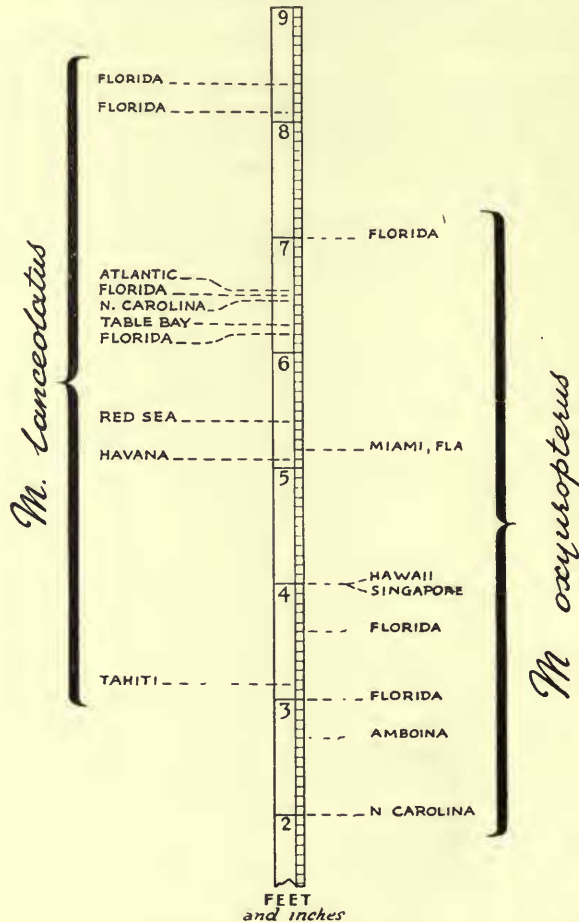

Fig. 12. Diagram showing comparative ranges of size for the two species of *Masturus*, based on recognizable records of adult specimens.

Mola mola Townsend 1918, *Bull. N.Y. Zool. Soc.* **21:** fig. (not of Linnaeus); Collett, 1896, *Résult. Camp. Sci. Monaco*, **10:** 163 (*part.*) pl. 6, fig. 1.

Mola lanceolata Schmidt, 1921, *Medd. Komm. Havundersøg. Kbh. Fisk.* **6** (6) (*part.*): pl. 1, fig. 6; Smedley, 1932, *Bull. Raffles Mus.* **7:** 17, pl.

Masturus lanceolatus Jordan & Jordan, 1925, *Mem. Carneg. Mus.* **10:** 89, fig. 7; Gudger & McDonald, 1935, *Sci. Mon.* **41:** 1, figs. 3, 10, 12, 13; Gudger, 1935, *Copeia*, **1935:** 35, figs. 1, 2; 1937, *Ann. Mag. Nat. Hist.* (10) **19:** 1 (*part.*), text-figs. 18, 22, 26, 27; 1937, *Proc. Zool. Soc. Lond.* **107** (A) (3): 353 (*part.*), text-figs. 5, 10, 12, 13, 15, 18 (?), 19, 22, pl. 1, figs. 1, 2, pl. 3, fig. 9 (?), pl. 4, fig. 11, pl. 5, fig. 17; 1939, *J. Elisha Mitchell Sci. Soc.* **15** (2): 305 (*part.*), figs.

1–5; Brimley, 1939, ibid. 300, pl. 29; Raven, 1939, *Bull. Amer. Mus. Nat. Hist.* **76** (4): 143, pl. 2; Hardenberg, 1939, *Treubia* **17** (2): 121; Clark, 1949, *Amer. Mus. Novit.* **1397**: 7, fig. 9.

A high proportion of the young specimens recorded seem to belong to this form, but a possible explanation of this is given on page 107. The small number of supporting rays in the caudal lobe, the equal bases of dorsal and anal fins, and the comparatively weak-looking 'chin' are recognizable even in McCulloch's 10-mm. specimen. The concavity of the dorsal profile of the head, however, is not noticeable in very small specimens, but it is already apparent in the 152-mm. example figured by Gudger (1939). The latter paper is also interesting in that it shows branching at the tips of the rays of the clavus, like that illustrated by Ryder (Fig. 7 A in this paper), but very much smaller, evidently in process of reduction. Only these two records of such branching exist, probably because the tips of the rays have been damaged in most small specimens, and the branching is lost with age.

This form is so often taken in the same locality as the preceding that it is almost certainly a sex of that species; in some instances young specimens of both forms have been taken from a single predatory fish (e.g. McCulloch (1912), whose 13-mm. specimen is *M. lanceolatus* and his 10-mm. specimen *M. oxyuropterus*; or Gudger (1939), whose 125-mm. fish is *M. oxyuropterus*, whereas at least the 127-mm. fish, and possibly the 130-mm. specimen also appears to be *M. lanceolatus*).

It will be noticed that in each case the *M. oxyuropterus* is slightly the smaller, and the records of this form do tend to lie about a lower range of size (Fig. 12). The largest record seems to be the 'Miami *Masturus* no. III' of Gudger, figured by Gudger & McDonald, though the identification of this badly slung specimen is a little doubtful. It was 7 ft. in length.

Recognizable records of adults of this form are from the Atlantic at North Carolina and Florida, from Singapore and Amboina, and from the Pacific at Hawaii. Young specimens have been taken at Florida, the Sargasso Sea, the Azores, and in the South Pacific.

A young specimen (Fig. 9) of unknown provenance is in our collection, and a plaster cast of the specimen dissected by Raven is exhibited in the fish gallery of the British Museum (Natural History).

Genus *MOLA* Koelreuter

Mola Koelreuter, 1770, *Novi Comment. Acad. Petropol.* **8**: 337. Type: *Mola aculeata* Koelreuter (= *Tetraodon mola* Linnaeus, young).

Orthragoriscus Bloch & Schneider, 1801, *Syst. Ichth.*: 510. Type: *Tetraodon mola* Linnaeus.

Cephalus Shaw, 1804, *Gen. Zool.* **5**: 437. Type: *Tetraodon mola* Linnaeus.

Orthragus Rafinesque, 1810, *Caratt. Sicilia*: 17. Type: *Orthragus luna* Rafinesque (= *Tetraodon mola* Linnaeus).

Diplanchias Rafinesque, 1810, ibid. Type: *Diplanchias nasus* Rafinesque.

Orthagoriscus Cuvier, 1817, *Règne Anim.*, ed. 1, **2**: 149. Type: *Tetraodon mola* Linnaeus.

Pedalion Swainson, 1839, *Nat. Hist. Fish.* **1**: 199. Type: *Pedalion gigas* (Guilding) Swainson.

Molacanthus Swainson, 1839, ibid. **2**: 329. Type: *Molacanthus pallasi* Swainson (= *Tetraodon mola* Linnaeus).

Ozodura Ranzani, 1839, *Novi Comment. acad. Sci. Inst. Bonon.* **3**: 80. Type: *Ozodura orsini* Ranzani.

Tympanomium Ranzani, 1839, ibid., table. Type: *Tympanomium planci* Ranzani.

Trematopsis Ranzani, 1839, ibid., table. Type: *Trematopsis willoughbii* Ranzani.

Pallasina Nardo, 1840, *Ann. Sci. Regno Lombardo-Veneto* **10**: 10, 112. Type: *Pallasina pallasi* Nardo (larval form).

Acanthosoma De Kay, 1842, *Nat. Hist. New York* (*Zool.*) **3**: 330. Type: *Acanthosoma carinatum* De Kay (= *Tetraodon mola* Linnaeus, young).

Aledon Castelnau, 1861, *Mém. Poiss. Afr. austr.*: 75. Type: *Aledon storeri* Castelnau.

Closely related to *Masturus*, but differing in that the clavus is supported entirely by elements from the dorsal and anal fins. The form of the body is relatively shorter, conspicuously so in the young, and the post-larval spines are not entirely lost, the base of one at the chin or one on the snout, or both, remaining as a low bony boss in the largest examples.

Very few post-larval specimens of *Mola* have been found, but the smallest, 5 mm. long, shows that there is an 'Ostracion boops' stage, and several examples of the secondary post-larval or 'Molacanthus' stage have been described; it is not known whether the 'cornicles' are ever as long as those of *Masturus*.

Although a number of naturalists have believed in the existence of several species of *Mola*, and Ranzani went so far as to recognize five genera and eleven species, it has generally been believed, especially during this century, that only one widely distributed species is admissible.

My studies, however, show that while *Mola mola* is indeed wide-ranging, it is largely or entirely replaced in the South Pacific by a second species, distinguishable as follows:

KEY TO THE SPECIES OF *MOLA*

I. Clavus supported by about 16 rays, 12 of which bear ossicles; the ossicles much broader than the spaces between them, and forming the margin of the clavus; those borne on paraxial rays separate, much smaller than the others. No band of reduced denticles between dorsal and anal fins   .   .   .   1. *ramsayi*

II. Clavus supported by about 12 rays, 8 or 9 of which bear ossicles; the ossicles widely separated, invested with cuticle, which grows beyond them to form lobes in large examples; those borne on paraxial rays united to form a single ossicle larger than all the others. A band of reduced denticles, smoother to the touch, at base of clavus from dorsal to anal fin   .   .   .   .   .   .   2. *mola*.

The term 'paraxial rays' refers to the pair of supporting rays of the clavus the proximal ends of which lie nearest to the end of the vertebral column. The smooth band between dorsal and anal fins in *M. mola* is usually visible, marked by a fold posteriorly, and often differently coloured from the rest of the fish; in doubtful cases the tips of the fingers will discern that this area is less rough than the body in front of it and the clavus behind it.

Mola ramsayi (Giglioli)

Orthagoriscus truncatus Hutton, 1872, *Fish. New Zealand*: 73. (Not of Fleming, 1828.)

Orthagoriscus mola Castelnau, 1872, *Proc. Zool. Acclim. Soc. Vict.* **1**: 211; 1875, *Res. Fish. Austral.*: 3; Hutton, 1873, *Trans. Proc. N.Z. Inst.* **5**: 271; Macleay, 1875, *Proc. Linn. Soc. N.S.W.* **1**: 12; Johnston, 1883, *Pap. Roy. Soc. Tasm.*: 137; 1891, ibid.: 38; Hamilton, 1886,

Trans. Proc. N.Z. Inst. **18:** 135; Williams, 1893, ibid. **25:** 110, pl. 8 *a*; Drew, 1897, ibid. **29:** 286; Parker, 1897, ibid.: 627; ? Fletcher, 1929, *Proc. Linn. Soc. N.S.W.* **54:** 225, 227. (Not of Cuvier, 1817.)
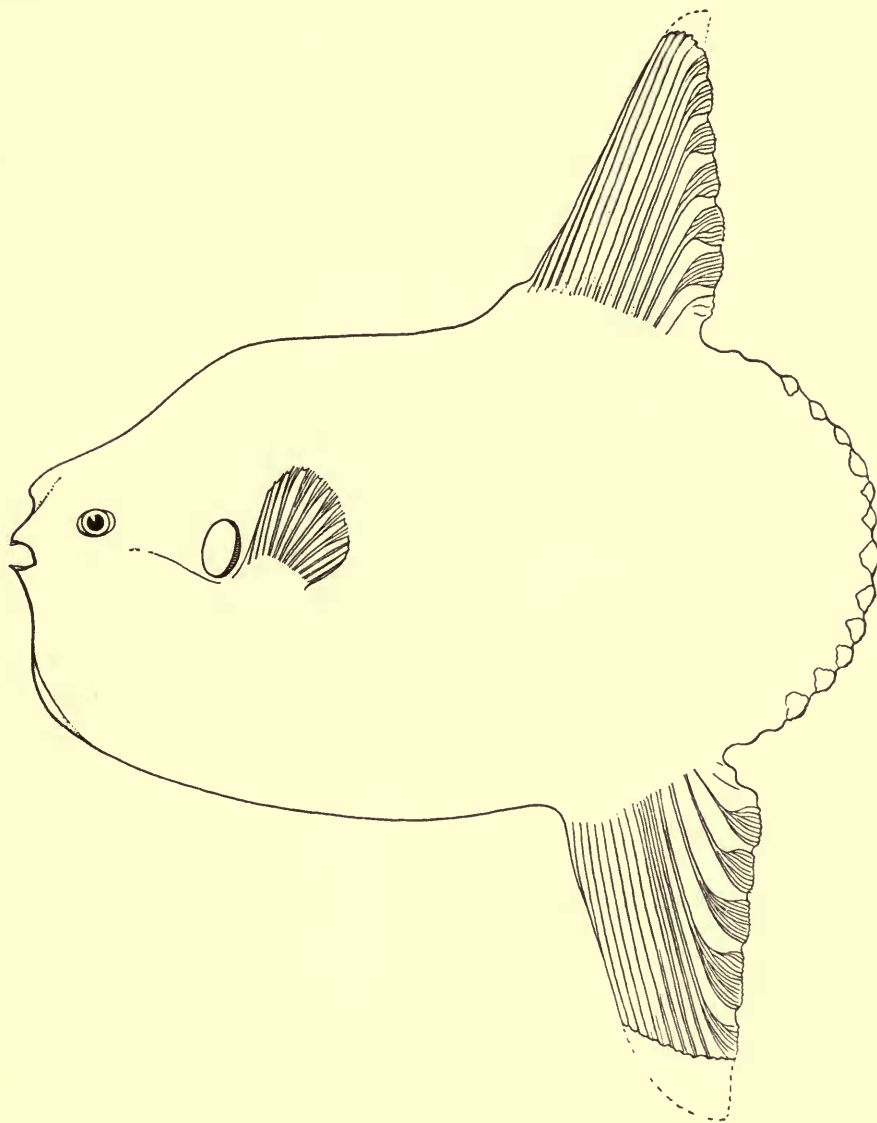

FIG. 13. *Mola ramsayi*, adult, 2130 mm. long, New South Wales. (Drawn from the type of the species in the British Museum collection.)

Orthragoriscus ramsayi Giglioli, 1883, *Nature, Lond.* **28:** 315; Ramsay, 1883, *Cat. N.S.W. Court. Intern. Fish. Exhib.*: 43.
? *Orthagoriscus eurypterus* Philippi, 1893, *Chilen. Fische*: 15, pl. 6, fig. 1 (not seen).
Mola mola Waite, 1907, *Rec. Canterbury* [*N.Z.*] *Mus.* **1:** 34; 1913, *Trans. N.Z. Inst.* **45:** 223, pl. 9; 1921, *Rec. S. Aust. Mus.* **2:** 198, fig. 332; 1923, *Fish. S. Austral.*: 230, fig.; Phillips, 1919,

Rep. Dom. Mus. N.Z.: 6; 1926, *N.Z. J. Sci. Tech.* **8** (3): 169, figs. 1–3; McCulloch, 1922, *Aust. Zool.* **2** (3): 130, fig. 374 *a*; 1930, *Mem. Aust. Mus.* **5** (3): 436 (*part.*); Schneider, 1930,
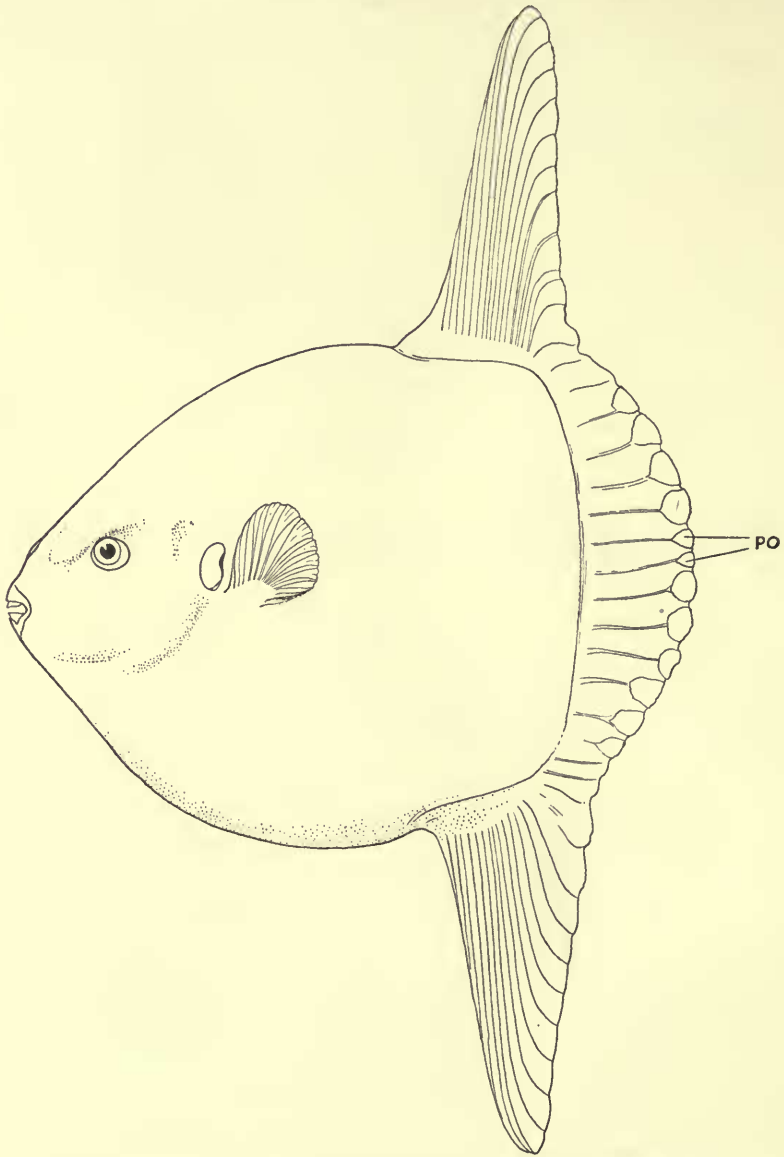

FIG. 14. *Mola ramsayi*, young adult, 410 mm. long, South Australia (?). (From specimen in spirits in the British Museum collection.)
PO, paraxial ossicles.

Rev. Chil. Hist. Nat. **34**: 200, figs. 36, 37; Fowler, 1945, ibid. **45–47**: 170, fig.; Morrow & Mauro 1950, *Copeia*, **1950**: 108, fig. 4 *c*.
Mola ramsayi Whitley, 1931, *Rec. Aust. Mus.* **18** (3): 126 (*part.*), pl. 16, figs. 3, 4.

All the New Zealand records, most of the Australian, and the few Chilean specimens appear to belong to this species, though in many cases it is not possible to be certain. It may be assumed, therefore, that in the South Pacific it replaces the wide-ranging *M. mola*. The two meet, however, in the Australian area, for Stead, McCulloch, and Whitley have all figured specimens which were undoubtedly *M. mola*, Whitley including his specimen with one of the true *M. ramsayi* in the same paper under the latter name.

The type of *Orthragoriscus ramsayi* Giglioli is in the British Museum (Nat. Hist.). Its locality was given as 'Southern Hemisphere', but a label accompanying the specimen states 'New South Wales', and it is known to have been taken on that coast (*fide* Whitley, 1931). It was exhibited at the International Fisheries Exhibition in London in 1883 and later presented to the Museum by the Commissioners of the Exhibition. It is a very large stuffed skin, now in a rather dilapidated condition. The total length is 213 cm. (6 ft. 8 in.).

We have, fortunately, a second specimen, in spirits—much smaller, of course; it is without a definite locality, but almost certainly from South Australia, since it was in a collection of specimens presented by the Zoological Society, several of which were typical South Australian species and all of which would be likely to occur there. It agrees very well with the excellent figure given by Waite (1923), and removes any doubt as to the distinctness of the species from *M. mola*.

The type is not by any means the largest recorded specimen of *M. ramsayi*. That distinction apparently goes to one taken on 12 December 1889 in Poverty Bay, and recorded by Williams as measuring 9 ft. 8 in. and weighing $3\frac{1}{2}$ tons.

Mola mola (Linnaeus)

Tetraodon mola Linnaeus, 1758, *Syst. Nat.* ed. 10, **1**: 334; Pennant, 1776, *Brit. Zool.* **3**: 131, pl.; Migliorini Spinola, 1843, *Poiss. Genes*: 14.

Tetrodon mola Brünnich, 1768, *Ichth. massil.*: 8; Gmelin, 1778, *Syst. Nat. Linn.*: 1447; Retzius, 1785; *K. Svensk. Vetensk. Akad. Handl.* **6**: 115; Bonnaterre, 1788, *Tabl. Encycl. Méth.*: 25, pl. 17, fig. 54; Lacepède, 1798, *Hist. Nat. Poiss.* **1**: 509; Retzius, 1800, *Fauna Suec.*: 310; Donovan, 1803, *Nat. Hist. Brit. Fish.* **2**: pl xxv.

Mola aculeata Koelreuter, 1770, *Novi Comment. Acad. Petropol.* **8**: 337.

Diodon mola Pallas, 1777, *Naturgesch. Thiere* **8**: 41, pl. 4, fig. 7; Bloch, 1785, *Naturgesch. ausländ. Fische* **1**: 75, pl. 128; Jacob. 1826, *Dublin Phil. J.* **2**: 443, pl.

Mola rotunda Cuvier, 1798, *Tabl. Elem. Nat. Hist.*: 323; Jordan, 1881, *Proc. U.S. Nat. Mus.*: 70; Jordan & Gilbert, 1883, *Bull. U.S. Nat. Mus.* **16**: 865; Petersen, 1884, *Vidensk. Medd. naturh. Foren. Kbh.*: 159; Smith, 1885, *W. Amer. Sci.* **1** (7): 45; Linton, 1897, *Proc. U.S. Nat. Mus.* **19**: 788, 812, 824; Steenstrup & Lütken, 1898, *K. Danske vidensk. Selsk. Skr.* (6) **9** (1): 28, pl. 1; Murray & Hjort, 1912, *Depths of the Ocean*: 119, 607, 615, 697, figs. 102, 507; Schmidt, 1921, *Medd. Komm. Havundersøg. Kbh. Fisk.* **6**: 1, figs. 1, 5, 6, 10 *b*, 12, pl. 1, figs. 1, 2; 1926, *Nature, Lond.* **117**: 80, figs. 1, 2; Ehrenbaum, 1936, *Handb. Seefisch. Nordeurop.* **2**: 86, fig. 68; Jensen, 1940, *Vidensk. Medd. nat. Foren. Kbh.* **104**: 319.

Orthragoriscus mola Bloch & Schneider, 1801, *Syst. Ichth.*: 510; Turner, 1862, *Nat. Hist. Rev.*: 185, pl. 6, figs. 4–6; Beneden, 1871, *Mém. Acad. R. Belg.* **38**; Jeude, 1890, *Notes Leyden Mus.* **12**: 189, pl.; Roon & Pelkwijk, 1939, *Zoöl. Meded. Leiden* **22**: 65, figs. 1, 2.

Orthragoriscus fasciatus Bloch & Schneider, 1801, *Syst. Ichth.*: 511.

Orthragoriscus hispidus Bloch & Schneider, 1801, ibid.: 511.

Cephalus brevis Shaw, 1804, *Gen. Zool.* **5**: 437, pl. 175; Neill, 1811, *Mem. Werner. Soc.* **1**: 546; Mitchill, 1815, *Trans. lit. phil. Soc. N.Y.* **1**: 471; Swainson, 1839, *Nat. Hist. Fish.* **1**: 199.

Cephalus pallasianus Shaw, 1804, *Gen. Zool.* **5**: 440.

Orthragus luna Rafinesque, 1810, *Caratt. Sicilia*: 17–18; *Indice Siciliana*: 40.

Diplanchias mola Rafinesque, 1810, ibid.

Cephalus mola Risso, 1810, *Ichth. Nice*: 60; Poey, 1868, *Repert. Cuba* **2**: 433.

Orthagoriscus mola Cuvier, 1817, *Regne Anim.*, ed. 1, **2**: 149; Fleming, 1828, *Hist. Brit. Anim.*: 175; Nilsson, 1832, *Prodr. Ichth. Scandinav.*: 111; Jenyns, 1835, *Man. Brit. Vertebr. Anim.*: 490; Storer, 1839, *Fish. Massachusetts*: 170, pl. 3, fig. 1; Swainson, 1839, *Nat. Hist. Fish.* **2**: 329, fig. 107; Bellingham, 1840, *Mag. Nat. Hist.* (N.S.), **4**: 235; Bennett, 1840, *Narr. Whaling Voy.* **2**: 262; Wellenbergh, 1840, *Dissert. Inaug., Lugd. Batav.*, pl.; Goodsir, 1841, *New Philos. J.* **30**: 188, pl. 4; De Kay, 1842, *Nat. Hist. N.Y.* (*Zool.*), **3**: 331, pl. 59, fig. 193; Storer, 1846, *Mem. Amer. Acad. Arts Sci.* N.S. **2**: 495; Dilwyn, 1848, *Mater. Fauna Swansea*: 15; Parlby, 1848, *Proc. Zool. Soc. Lond.* **17**: 6; 1850, *Ann. Mag. Nat. Hist.* (2) **5**: 53; Schlegel, 1850, *Fauna Japonica* (*Poiss.*): 288, pl. 127; Costa, 1850, *Fauna Regn. Napoli* (*Pesci, Plettognathi*): 28, pls. 63–64; Smith, 1851, *Ann. Mag. Nat. Hist.* (2) **8**: 347; Kroyer, 1852, *Danmarks Fisk.* **3**: 732; Embleton, 1854, *Trans. Tyneside Nat.* **2**: 110, pl. 3; Nilsson, 1855, *Skandinav. Fauna*: 697; Thompson, 1856, *Nat. Hist. Ireland* **4**: 243; Kölliker, 1860, *Verh. phys-med. Ges. Würzburg* **10**: xxxviii; Cleland, 1862, *Nat. Hist. Rev.*: 170, pl. 5–6; Storer, 1863, *Mem. Amer. Acad. Arts Sci.* N.S. **8** (2): 420, pl. 34, fig. 2; Beltremeux, 1864, *Ann. Acad. la Rochelle* (*Faune*): 53; Couch, 1865, *Hist. Fish. Brit. Is.* **4**: 377, pl. 245; Blanchere, 1868, *Nouv. Dict. pêches*: 505, fig. 673; Schlegel, 1869, *Nat. Hist. Ned. Vischen*: 182, pl. 17, fig. 4; Günther, 1870, *Cat. Fish. Brit. Mus.* **8**: 317; Capello, 1870, *J. Sci. Math. Phys. Nat. Lisboa* **2**: 136; 1881, *Mem. R. Acad. Lisboa*: 41; Andrews, 1871, *Proc. Nat. Hist. Soc. Dublin* (1865–1869), **5** (1): 123; Putnam, 1871, *Proc. Amer. Ass. Adv. Sci.* **19**: 255; *Amer. Nat.* **4**: 629, figs. 134, 137; Jourdain, 1871, *C. R. Acad. Sci. Paris* **63**: 1225; Canestrini, 1872, *Fauna d'Italia* (*Pesci*): 148; Barker, 1876, *Zoologist*: 5087; Malm, 1877, *Göteborgs Fauna*: 599, 654; Winther, 1879, *Nat. Tidsskr.* (3) **12**: 54; Stossich, 1879, *Boll. Soc. Adriat. Sci. Nat.* **5**: 36; Moreau, 1881, *Poiss. France* **2**: 74; Vignal, 1881, *Arch. Zool. exp. gén.* **9**: 369, pl. 21; Campbell, 1883, *Proc. Nat. Hist. Soc. Glasgow* (1882) **5**: 176; Day, 1884, *Fish. Gt. Brit.* **2**: 272, pl. 148; Thompson, 1888, *Anat. Anz.* **3**: 93, figs.; 1889, *Stud. Mus. Zool. Univ. Coll. Dundee* **1**, No. 4; Vinciguerra, 1890, *Boll. Mus. Zool. Rome* **1**: 33; Haller, 1891, *Morph. Jb.* **17**: 198, figs., pls. 13–15; Steindachner, 1891, *Ann. Naturh. Hofmus. Wien* **6**: 90; Almeida & Roquette, 1892, *Inquir. Industr., Lisboa* **2**: 377; Girard, 1894, *Ann. Sci. Nat., Porto* **1**: 31; Tagliani, 1894, *Monit. Zool. ital.* **5**: 248; Grieg, 1895, *Bergens Mus. Aarb.* **6**: 11; Smitt, 1895, *Skandinav. Fisk.* **2**: 622, figs. 153, 154 a, 156, 157, pl. 27, fig. 4; Osorio, 1896, *J. Sci. Math. Phys. Nat. Lisboa* **4**: 157; Vieira, 1898, *Ann. Sci. Nat., Porto*: 24; Clarke, 1898, *Zoologist* **16**: 439; Andersson, 1900, *Öfvers. Vetensk Akad. Förh., Stockh.*: 603; Parker, 1900, *Anat. Anz.* **17**: 313, fig.; Herdman & Dawson, 1902, *Mem. Lancs. Sea Fish. Comm.* **2**: 57; Griffini, 1903, *Ittiol. Ital.*: 155, figs. 81, 82; Michailovskij, 1903, *Annu. Mus. Zool., Acad. St. Pétersb.* **8**: xlvi; Meek, 1904, *Anat. Anz.* 25: 217, fig.; Dall, 1908, *Bull. Mus. Comp. Zool. Harv.* **43** (6): 232; Novikov, 1909, *Dnevn. russkh. Estestroisp.* **1909–1910**: 286; 1910, *Anat. Anz.* **37**: 97; Sauvage, 1910, *Mém. Soc. Hist. Nat. Autun.* **23**: 1; Günther, 1910, *J. Mus. Godeffroy* **9** (17): 477; Seabra, 1911, *Bull. Soc. Portug. Sci. Nat.*: 193; Le Danois, 1913, *Poiss. Manche occ.*: 106, fig. 182; Kaschkarov, 1916, *Rev. Zool. Russe* **1**: 110, figs. 1–12; Thompson, 1918, *Scot. Nat.*: 41, 59; Kincaid, 1919, *Annot. List. Puget Sound Fish.*: 23, fig. 43; Toni, 1921, *Atti Ist. Veneto* **80**: 125; Grenholm, 1923, *Stud. Floss. Teleost. Upsala*: 240; Patroni, 1923, *Ann. Mus. zool. Napoli*, N.S. **5** (4), pl. 1; Jenkins, 1925, *Fish. Brit. Is.*: 212, pl. 85; Duncker & Mohr, 1926, in Grimpe & Wagler, *Tierwelt Nord u. Ostsee* **4** (12): XIIg 29, figs. 4, 5; Gudger, 1928, *Sci. Mon. N.Y.*: 257; Burr, 1928, *J. Comp. Neurol.* **45**: 33, figs.; Caraffa, 1929, *Poiss. Corse*: 50, fig.; Marine Biol. Ass. 1931, *Plymouth Mar. Fauna*: 318; Saemundsson, 1931, *Nat. Reykjavik* **1**: 164; 1939, *Vidensk. Medd. naturh. Foren. Kbk.* **102**: 207; Noronha & Sarmento, 1934, *Peixes Madeira*: 121; Nobre, 1935, *Fauna Mar. Portugal, Vertebr.*: 240, fig. 109; Toschi, 1936, *Boll. Pesca Piscicolt. Idrobiol.* **12**: 325; Sanzo, 1939, *Arch.*

zool. Torino **26**: 121, pl. 7, figs. 16, 17; Andersson, 1942, *Fisk. Nord.* **1**: 62, pl.; Roon, 1942, *Zoöl. Meded.* **23**: 313, fig.

Orthagoriscus spinosus Cuvier, 1817, *Régne Anim.* ed. 2, **2**: 370; Richardson, 1844, *Voy. Sulphur, Fish.*: 125, pl. 62, figs. 10–12.

Cephalus ortagoriscus Risso, 1826, *Hist. eur. Mérid.* **3**: 173.

Diodon carinatus Mitchill, 1828, *Ann. Lyceum New York* **2**: 264, pl. 5, fig. 1.

? *Mola aspera* Nardo, 1828, *Bull. Sci. Nat. (Férussac)* **8**: 437; Bonaparte, 1846, *Cat. met. pesci eur.*: 87.

Mola hispida Nardo, 1828, ibid.: 438.

Pedalion gigas (Guilding) Swainson, 1839, *Nat. Hist. Class. Fish.* **1**: 199, fig. 33.

Molacanthus pallasi Swainson, 1839, ibid. **2**: 329.

Ozodura orsini Ranzani, 1839, *Novi Comment. Acad. Sci. Inst. Bonon* **3**: 80, pl. 6.

Tympanomium planci Ranzani, 1839, ibid., table.

Diplanchias nasus Ranzani, 1839, ibid.

Trematopsis willughbii Ranzani, 1839, ibid.

Orthragoriscus retzii Ranzani, 1839, ibid.; Bonaparte, 1846, *Cat. met. pesci eur.*: 87.

Orthragoriscus ghini Ranzani, 1839, ibid.

Orthragoriscus rondeletii Ranzani, 1839, ibid.

Orthragoriscus blochii Ranzani, 1839, ibid.

Orthragoriscus alexandrini Ranzani, 1839, ibid., pl. 6; Alessandrini, 1839, ibid.: 359, pls. 31–34.

Orthragoriscus redi Ranzani, 1839, ibid., table.

Orthragoriscus aculeatus Ranzani, 1839, ibid.

Pallasina pallasi Nardo, 1840, *Ann. Sci. Regno Lombardo-Veneto* **10**: 112.

Acanthosoma carinatum De Kay, 1842, *Nat. Hist. New York, Zool.* **3**: 330, pl. 15, fig. 179; Storer, 1846, *Mem. Amer. Acad. Arts Sci.* **2**: 494.

Molacanthus hispidus Bonaparte, 1846, *Cat. met. pesci eur.*: 87.

Mola luna Sassi, 1846, *Saggio sopr. Pesci,* &c.: 35; Aradas, 1871, *Ann. Min. Agric. Ind. Comm.* **1**, pt. 1: 587.

Orthagoriscus analis Ayres, 1859, *Proc. Calif. Acad. Sci.* **2**: 31, fig. 14; 1860, ibid.: 54, fig. 5; Stearns 1867, ibid. **3**: 341.

Molacanthus carinatus Gill, 1861, *Proc. Acad. Nat. Sci. Philad.* (1860): 21.

Aledon storeri Castelnau, 1861, *Mém. poiss. Afr. australe*: 75.

Aledon capensis Castelnau, 1861, ibid.: 76.

Mola nasus Steenstrup & Lütken, 1863, *Overs. danske Vidensk. Selsk. Forh.*: 36; Wahlgren, 1868, *Acta Univ. Lund.* **4**: 1, pl.

Mola retzii Steenstrup & Lütken, 1863, ibid.; Wahlgren, 1868, ibid.

Orthagoriscus sp. Swinhoe, 1863, *Ann. Mag. Nat. Hist.* (3) **12**: 225.

Orthagoriscus ozodura Harting, 1868, *Verh. Akad. Wet. Amst.* **11**: 1, pls. 1–8.

Orthagoriscus planci Stossich, 1879, *Boll. Soc. Adriat. Sci. Nat.* **5**: 36.

Orthagoriscus nasus Jeude, 1892, *Notes Leyden Mus.* **14**: 127, pl. 5; *Tijdschr. Ned. Dierk. Ver.* **18**: 185, pl. 11.

Orthagoriscus sp. Reuvens, 1894, *Notes Leyden Mus.* **16**: 128, pl. 5.

Mola mola Jordan, 1885, *Proc. U.S. Nat. Mus.* **8**: 393; Eigenmann, 1893, ibid. **15** (1892): 131, 175; Jordan, 1895, *Proc. Calif. Acad. Sci.* (2) **5**: 491; Collett, 1896, *Résult. Camp. Sci. Monaco*, **10**: 163 (*part.*); Jordan & Evermann, 1898, *Bull. U.S. Nat. Mus.*, No. 47, **2**: 1753; H. M. Smith, 1898, *Bull. U.S. Fish. Comm.* **17**: 85; Linton, 1898, *Proc. U.S. Nat. Mus.* **20**: 507 et seq.; Evermann & Kendall, 1899, *Rep. U.S. Fish. Comm.*: 88; Jordan & Snyder, 1901, *Proc. U.S. Nat. Mus.* **24**: 260; Green, 1901, *Bull. U.S. Fish. Comm.* **19**: 321; Jordan & Evermann, 1902, *Amer. Food and Game Fish.*: 492, fig.; Gilbert & Starks, 1904, *Mem. Calif. Acad. Sci.* **4**: 206; Hargitt, 1905, *Bull. U.S. Bur. Fish.* **24** (1904): 25; Stead, 1906, *Fish. Austral.*: 227, fig. 82; Starks & Morris, 1907, *Univ. Calif. Publ. Zool.* **3** (11): 205; Murray & Hjort, 1912, *Depths of the Ocean*: 644; Halkett, 1913, *Checklist Fish. Canada*: 116; Dean, 1913, *Amer. Mus. J.* **13** (8): 370, fig.; Hilton, 1914, *J. Ent. Zool.* **6** (4): 233; Evermann, 1915, *Copeia*, **20**: 17; Buen, 1919, *Bol. Pesc. Madr.* **4**: 295; 1935, *Notas. Inst. esp. Oceanogr.* **2** (89): 146; Dons, 1920,

Troms. Mus. Aarsh. **43** (6): 38, pl. 2; Jordan, 1921, *Copeia*, **93**: 28; McCulloch, 1922, *Aust. Zool.* **2**: 130, pl. 43, fig. 374 *a*; Fowler, 1923, *Proc. Acad. Nat. Sci. Philad.* **75**: 294; Wolleboek, 1924, *Norges Fiske*: 224, fig. 254; Damant, 1925, *Nature, Lond.* **116**: 543, fig.; Bigelow & Welsh, 1925, *Bull. U.S. Bur. Fish.* **40** (1): 301; Buen, 1926, *Résult. Camp. int. Inst. esp. Oceanogr.* **2**: 56; Barnard, 1927, *Ann. S. Afr. Mus.* **21**: 986; Fowler, 1928, *Mem. Bishop Mus.* **10**: 473; Ulrey & Greeley, 1928, *Bull. Calif. Acad. Sci.* **27** (1): 24; Breder, 1929, *Field Book Mar. Fish. Atlant. Coast*: 236, fig.; Hubbs & Schultz, 1929, *Calif. Fish Game*, **15** (3): Ulrey, 1929, *J. Pan-Pacif. Res. Inst.* **4** (4): 11, 235; McCulloch, 1930, *Mem. Aust. Mus.* **5**: 436; Myers & Wales, 1930, *Copeia* **1934**: 11; Ancona, 1931, *Faune Flore Mediter.*, figs. 1, 2; Breder, 1932, *Copeia* (4): 180; Gregory, 1933, *Trans. Amer. Phil. Soc.* **23** (2): 294; Gregory & Raven, 1934, *Copeia* **4**: 145; Barnard, 1935, *Ann. S. Afr. Mus.* **30**: 645; Barnhart, 1936, *Mar. Fish. South. Calif.*: 95, fig. 288; Tibby, 1936, *Calif. Fish Game* **22** (1): 49, fig. 22; Fowler, 1936, *Bull. Amer. Mus. Nat. Hist.* **170** (2): 1123, fig. 469; Schultz & De Lacy, 1936, *Mid-Pac. Mag.* **49** (3): 211; Scofield, 1937, *Calif. Fish Game* **23** (4): 336; Schultz, 1938, *Nat. Geogr. Mag.* **74** (4): 497; Brimley, 1939, *J. Elisha Mitchell Sci. Soc.* **15** (2): 301, pl. 30; Deranyigala, 1944, *J. Bombay Nat. Hist. Soc.* **44** (3): 429; Mendes, 1944, *Bol. Fac. Filos. Cien. Let. Univ. S. Paula, Zool.* No. 8: 173, pl.; Engel, 1945, *Zoöl. Meded. Leiden* **25**: 11, pl. 1; Clemens & Wilby, 1946, *Bull. Fish. Res. B. Canada* **68**: 330, fig..247; Medcof & Schiffman, 1947, *Acadian Nat. New Brunswick* **2**: 8, 63, fig.; Poll, 1947, *Poiss. Mar.*: 405, figs. 260, 261; Barnard, 1948, *Ann. S. Afr. Mus.* **36** (5): 401, pls. 12, 13; Maul, 1949, *Vertebr. Madeira*, ed. 2, **2** (Peixes): 158; Clark, 1949, *Amer. Mus. Novit.* **1397**: 7, fig. 9; J. L. B. Smith, 1949, *Sea Fish. S. Africa*: 422, pl. 95, fig. 1213; Tortonese, 1950, *Att. Acc. Ligure Sci.* **6** (1): 112.

Orthragoriscus nasus Reuvens, 1897, *Notes Leyden Mus.* **18**: 209, pl. 3.

Mola ramsayi Whitley, 1931, *Rec. Aust. Mus.* **18** (3): 126 (*part.*), fig. 2, pl. 16, fig. 1; 1933, *Vict. Nat.* **49**: 210, figs. 1, 2 (not of Giglioli).

Mola alexandrini Barnard, 1948, *Ann. S. Afr. Mus.* **36** (5): 402.

The above extensive synonymy illustrates the considerable literature which has accumulated concerning this species. From a perusal of this data it is possible to give a rather more complete account than for other members of the family, but there is still much of its biology that remains conjectural. The anatomy has been studied broadly and in detail by a number of workers, and from this, together with descriptions or figures giving reliable information about the clavus, it seems quite clear that not more than one species is involved. Published records, considered statistically, would give the impression that the species is mainly a North Atlantic one, becoming rarer southwards, in the Indian Ocean and in the Western Pacific, but this is possibly an illusion due to the much higher rate of publication in the Atlantic and Mediterranean countries.

Certainly the Japanese form is not separable from the Atlantic form, since we have specimens from Japan in our collection for comparison; according to Jordan and Fowler it occurs at Hawaii, and it seems to be common at California, so that it is replaced by *M. ramsayi* only in the South Pacific. I am much indebted to Mr. W. I. Follett, of the California Academy of Sciences, for information and radiographs which enable me to identify the Californian specimens.

A bad practice among some authors is the borrowing of an illustration from some earlier work, especially when the specimen depicted was obtained in a locality remote from that being discussed. *Mola mola* has suffered much from this treatment, and in consequence it is not possible to be definite as to the identity of specimens in regions where *M. ramsayi* might occur also, because the distinguishing characters

of the clavus have been hitherto unknown and are, therefore, not described; a reliable picture might have given the answer.

Comparison of adequate descriptions and figures shows that some order underlies the variability which has been remarked upon by so many authors. After metamorphosis the young fishes are short and deep, the snout not protuberant, the fins rather narrow, and the margin of the clavus is not conspicuously lobed. The length of the clavus from the posterior edge of the 'carapace'—i.e. the anterior edge of the smooth band between dorsal and anal fins—is much less than that of the head. When the fish exceeds a length of about 2 ft., however, sexual differences become apparent. The bony tubercle on the snout is either pushed forward (in the male), or upward (in the female); in consequence the male develops a pronounced snout, projecting forward (the '*nasus*' form), while the female appears more deep-headed, with the front of the snout nearly vertical (the '*alexandrini*' form). As growth proceeds the clavus develops backwards between the ossicles, forming a series of lobes which at first number between 9 and 12 in both sexes; females do not seem to pass beyond this stage, but in large males the five median lobes become very large and the others reduced. After the formation of the lobes the clavus is probably always longer in a male than in a female of the same size, and in the biggest males it may be as long as the head. In large specimens of both sexes two prominent, swollen ridges are formed on each side of the head; these are discernible in small examples, and are evidently analogous if not homologous with the lateral ridges of Ostracionts, but with age they become very conspicuous. In the larger examples also the dorsal and anal fins are relatively much broader.
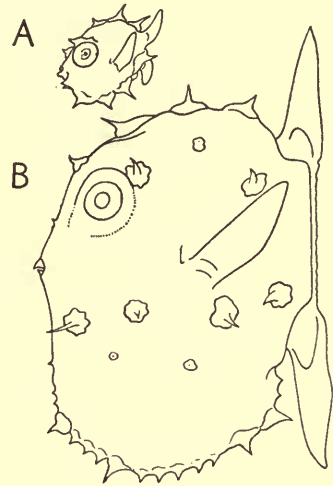

FIG. 15. Post-larvae of *Mola*. A. '*Ostracion boops*' stage (5 mm.). (After Schmidt); B. '*Molacanthus*' stage (16 mm.). (From specimen in the British Museum collection.)

All this is indicated by a study of the records. Comparatively few of the specimens described have been examined for sex, but in each case where the sex is stated the characters mentioned above are found to be associated with it; of particular interest is the paper by Roon & Pelkwijk (1939), who had both sexes and figured them together. Harting's (1868) plate 1 gives a fair representation of a female, and Whitley (1931) has given a drawing of another, together with a photograph of it (pl. xvi, fig. 1), which shows the lateral ridges excellently, and Murray & Hjort's (1912) photograph, copied by Schmidt, illustrates a fine male. The various phases of development outlined do not always coincide with a particular size or age, but are evidently dependent to some extent on environmental circumstances.

Mola mola grows to a great size, the largest record being apparently that by Dean (1913), measuring 10 ft. 1 in. in length and 11 ft. from tip of dorsal fin to tip of anal fin, a male. Mikailovskij (1903) described one measuring 8 ft. 6 in. in length and weighing 1,410 kg. Jeude (1890) described a specimen 2·23 m. (7 ft.) in length,

apparently a female. The specimen recorded by Günther as '7 feet long, Portsmouth' was the fish taken by Parlby (1849), who described its capture at Chesil Beach and
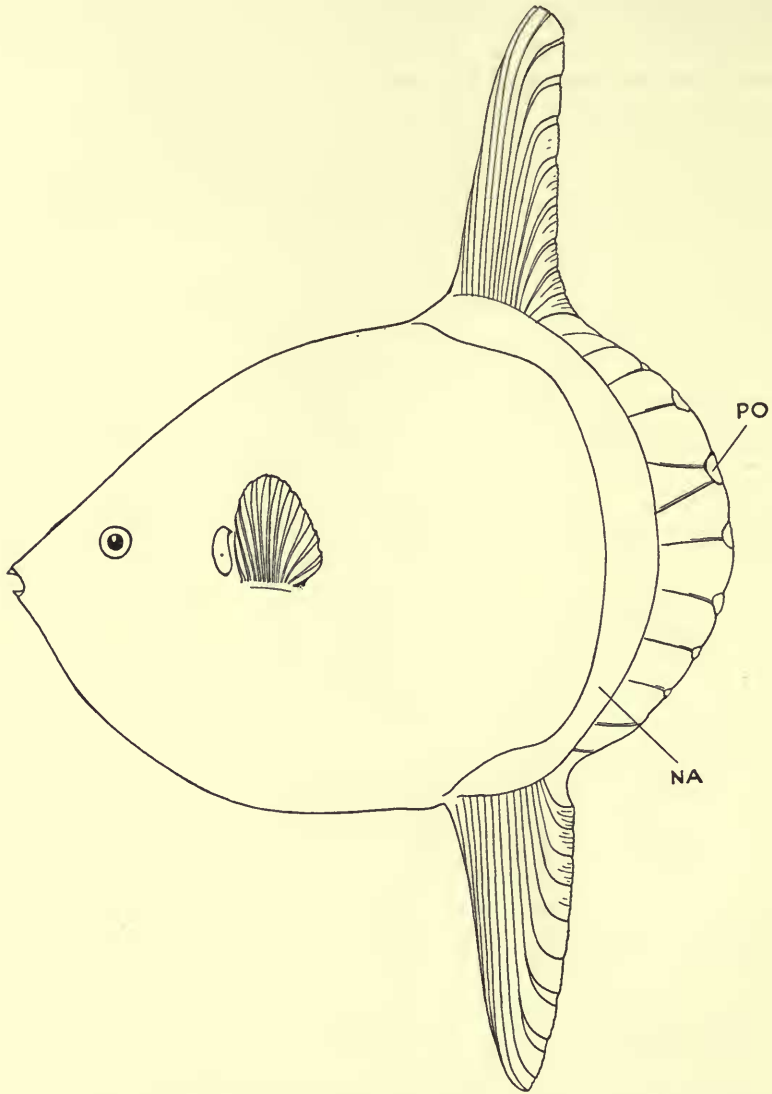

FIG. 16. *Mola mola*, adult, 600 mm. long, Plymouth. (From stuffed specimen in the British Museum collection.)

NA, area of reduced denticles; PO, paraxial ossicle.

stated that it measured 6 ft. 3 in. long. It was probably a male. As a stuffed skin it remained in the British Museum collection until recently, when it was found to be in a bad state and destroyed; my (calliper) measurement at this time reading 5 ft. 8 in., the loss being presumably due to shrinkage (unless Parlby made a contour measure-

ment). A number of smaller stuffed skins and several specimens in spirits remain in the collection. It is never common, the large literature being due to the great interest
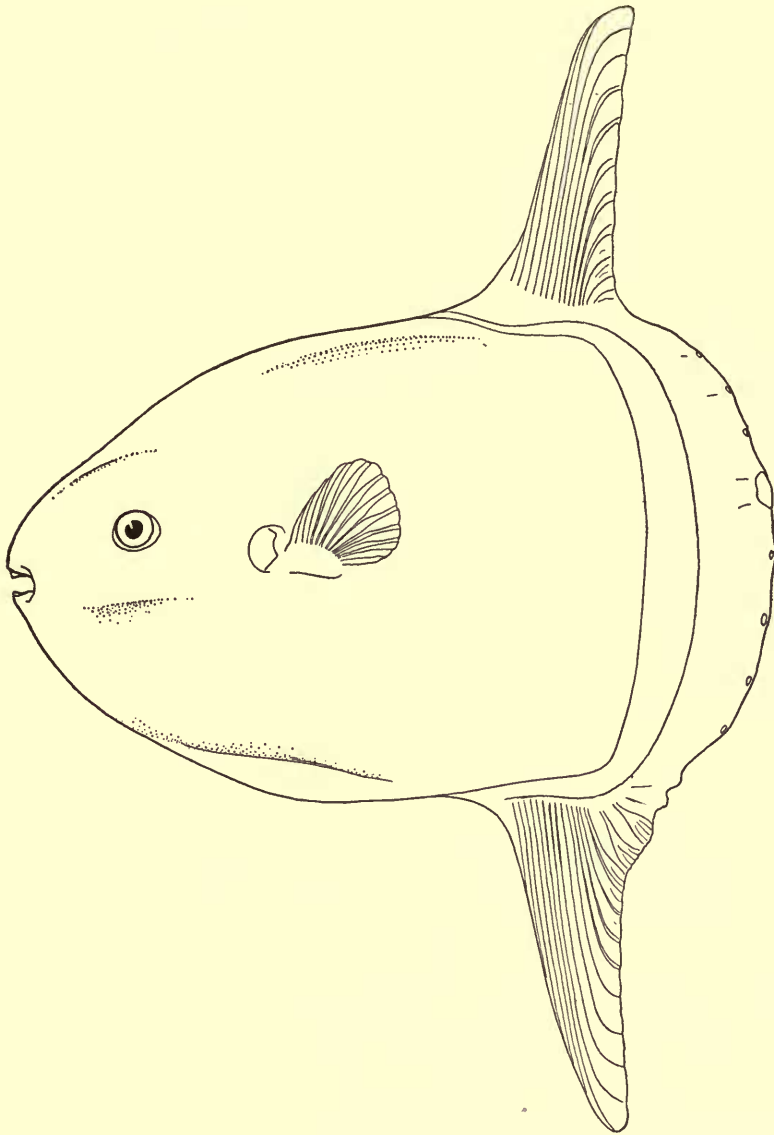
FIG. 17. *Mola mola*, young adult, 366 mm. long, Chouse, Japan. (From specimen in spirits in the British Museum collection.)

it arouses, almost every specimen being reported upon; but it is more frequently met with than any of the previous species. Nevertheless its early developmental stages are less well known than those of *Ranzania*, and fertile eggs or early larvae have not been found; it is not improbable that it spends a great part of its life in deep water.

The scarcity of young specimens is remarkable when we consider that a female 4 ft. 6 in. long contained 300 million eggs. The mode and place of breeding have yet to be found.

Its migrations inshore are unpredictable, and are usually supposed to coincide with invasions of medusae, salps, and ctenophores, upon which it largely feeds. Specimens
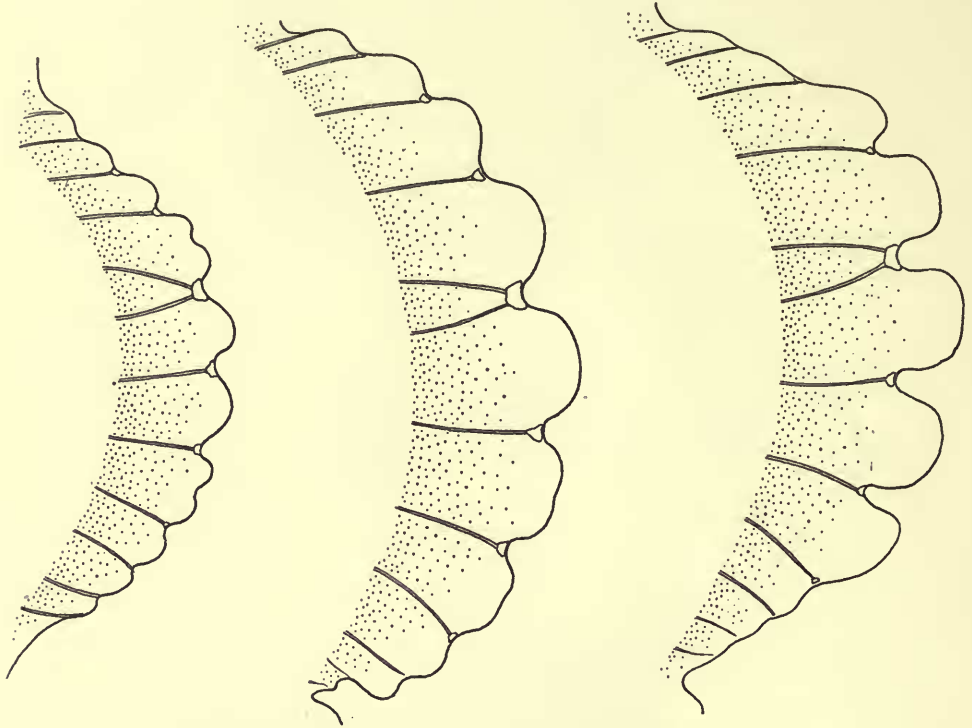

Fig. 18. Different lobulation of the clavus, with similar skeletal supports, in *Mola mola*. Drawn to the same size for comparison. That on the right is the characteristic form in large males.

taken inshore, however, are usually found to be feeding on littoral forms, and the list of organisms taken from stomachs includes crustacea, ophiuroids, molluscs, hydroids, ctenophores, corallines, and algae; Schmidt has reported them as feeding heavily on *leptocephali*; on one occasion a flounder (*Platichthys flesus*) was found in the throat (Reuvens, 1897), and in our collection there is a ling (*Molva macrophthalma*) two feet long which was taken from the stomach of *Mola mola*. The stomach is not infrequently found to be empty, and it is quite probable that the specimens so frequently taken without difficulty while 'basking' at the surface are in fact sick or dying fish. Myers & Wales (1930) found young fish to be active and alert, but later found two larger fish 'disabled' at the surface. It would be interesting to know the cause of such disablement. Possibly the great variety of parasites with which they are often found to be infested may have some bearing on the matter.

REFERENCES

BARNARD, K. H. 1927. A Monograph of the Marine Fishes of South Africa. Part II. *Ann. S. Afr. Mus.* **21** (2): 419–1065. (Molidae, p. 984.)

—— 1935. Notes on South African Marine Fishes. *Ann. S. Afr. Mus.* **30** (5): 645–658, pls. 23–25. (Molidae, p. 635, figs. 5–7.)

CHABANAUD, P. 1935. Quelques Monstruosités chez des Poissons Hétérosomes. *Arch. Mus. Hist. Nat. Lyon*, **15**: 1–23, 4 pls.

FRASER-BRUNNER, A. 1943. Notes on the Plectognath Fishes. VIII. The Classification of the Suborder Tetraodontoidea, with a Synopsis of the Genera. *Ann. Mag. Nat. Hist.* (11) **10**: 1–18.

GREGORY, W. K., & RAVEN, H. C. 1934. Notes on the Anatomy and Relationships of the Ocean Sunfish (*Mola mola*). *Copeia*, No. 4: 145–151, pl.

GREEN, E. H. 1901. The Chemical Composition of the Sub-dermal Tissue of the Ocean Sunfish. *Bull. U.S. Fish Comm.* **19**: 321.

GUDGER, E. W. 1937 *a*. The Structure and Development of the Pointed Tail of the Ocean Sunfish *Masturus lanceolatus*. *Ann. Mag. Nat. Hist.* (10) **19**: 1–46, pls. 1–2.

—— 1937 *b*. The Natural History and Geographical Distribution of the Pointed-tailed Sunfish (*Masturus lanceolatus*) with Notes on the Shape of the Tail. *Proc. Zool. Soc. Lond.* (A) pt. 3: 353–396, pls. 1–4.

McCULLOCH, A. R. 1912. A Description and Figures of Three Specimens of *Molacanthus*. *Proc. Linn. Soc. N.S.W.* **37**: 553–555, 2 pls.

PELLEGRIN, J. 1912. Sur la présence d'un banc de *Ranzania truncata* Retzius à la Martinique. *Bull. Soc. Zool. France*, **37**: 228–230, fig. 1.

RAVEN, H. C. 1939 *a*. Notes on the Anatomy of *Ranzania truncata*. *Amer. Mus. Novit.* **1038**: 1–7.

—— 1939 *b*. On the Anatomy and Evolution of the Locomotor Apparatus of the Nipple-tailed Sunfish (*Masturus lanceolatus*). *Bull. Amer. Mus. Nat. Hist.* **76** (4): 143–150, pl. 2.

RYDER, J. A. 1886. On the Origin of Heterocercy and the Evolution of the Fins and Fin-rays of Fishes. *Rep. U.S. Fish Comm.* 1884: 981–1085, 11 pls.

SANZO, L. 1939. Rarissimi stadi larvali di Teleostei. V. *Orthagoriscus mola* Linn. *Arch. zool. Torino* **26**: 143–146, pl. 7, figs. 16–17.

SCHMIDT, J. 1932. *Dana's Togt omkring Jorden. 1928–30.* 368 pp. (Molidae, p. 249 et seq.) København.

TREWAVAS, E. 1933. On the Structure of Two Oceanic Fishes, *Cyema atrum* Günther and *Opisthoproctus soleatus* Vaillant. *Proc. Zool. Soc. Lond.* (3): 601–614, 2 pls.

WHITLEY, G. P. 1931. Studies in Ichthyology No. 4. *Rec. Aust. Mus.* **18** (3): 96–133, pls. 11–16. (Molidae, p. 126, fig. 2, pl. 16.)